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CHEILOSTOMATOUS POLYZOA FROM THE UPPER BRACKLESHAM BEDS (EOCENE) OF SUSSEX

A. H. CHEETHAM

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CHEILOSTOMATOUS POLYZOA FROM THE UPPER BRACKLESHAM BEDS (EOCENE) OF SUSSEX

BY

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CHEILOSTOMATOUS POLYZOA FROM THE UPPER BRACKLESHAM BEDS (EOCENE) OF SUSSEX

By A. H. CHEETHAM

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SYNOPSIS

Thirty-eight species distributed in 34 genera of Cheilostomata are identified in a collection of Polyzoa from the Upper Bracklesham Beds at Selsey, Sussex. All the species, including ten new ones and two left *nomina aperta*, are described, and several of the genera to which they belong are diagnosed. One species is re-named.

The stratigraphical and geographical ranges of the Upper Bracklesham species are compiled from the literature and are used, together with the relative abundances of colonial growth forms, to interpret the stratigraphy and palaeoecology of the Upper Bracklesham Beds and the palaeogeography of the Hampshire Basin in Late Eocene times. The morphology of the Upper Bracklesham Cheilostomata, especially their zoarial habits and the linear dimensions of their zooecia and heterozooecia, are discussed.

I. INTRODUCTION AND ACKNOWLEDGMENTS

The Eocene Polyzoan fauna of England contrasts so markedly in both abundance and diversity with that of the Continent that Vine (1889 : 156) at one time considered it doubtful that Polyzoa would ever be discovered in quantity in the British Lower Tertiaries. However, Gregory (1893), Davis (1928, 1929*a*, 1934, 1936*a*, 1936*b*, 1940, 1962), Burton (1929), and Thomas & Davis (1949) have since reported from the Eocene strata of both the London and Hampshire Basins a number of Polyzoa, including a total of 58 nominal species, with an additional 13 left *nomina aperta*, of Cheilostomata : 29 species from the London Clay, 29 species from the Lower

Bracklesham Beds, and 15 species from the Barton Beds. Only six species of Cheilostomata—*Biselenaria offa* Gregory, *Cellepora petiolus* Lonsdale, *Heterocella* sp., *Lunulites transiens* Gregory, *Poricellaria alata* d'Orbigny and *Teichopora clavata* Gregory (Lonsdale 1850, Gregory 1893, Davis 1962)—have been known to occur, heretofore, in the Upper Bracklesham Beds.

On the other hand, more than 125 nominal species, a number of them doubtless synonyms, have been identified among the Cheilostomata from the Eocene beds of the Paris Basin (Buge 1946), most of them from the Lutetian and Auversian Stages. Such characteristic French Eocene genera as *Caberoides* Canu, *Dakaria* Jullien, *Entomaria* Duvergier, *Gaudryanella* Canu, *Hippoporina* Neviani, *Kionidella* Koschinsky and *Tubucella* Canu & Bassler have not so far been reported in co-eval faunas in Britain.

In November 1961 Mr. Dennis Curry presented to the British Museum (Natural History) an unsorted collection of Polyzoa from the Upper Bracklesham Beds at Selsey, Sussex. The task of sorting and studying this collection was undertaken in December 1961 and continued intermittently through 1964. Thirty-eight species belonging to 34 genera have been identified among the Cheilostomata, and a less diversified assemblage of Cyclostomata, not treated here, awaits investigation.

This work fills a gap in the stratigraphical record of British Cheilostomata and permits fresh interpretation of the history of Anglo–Franco–Belgian Polyzoan faunas. The study has been complicated by the scattered, in many cases vague, descriptions and long synonymies of the Continental Eocene Cheilostomata and by some still controversial aspects of British–European stratigraphical correlation. The modern works of Curry (1958*a*, 1958*b*, 1962, 1962 MS.), Davis & Elliott (1957), and Wrigley & Davis (1937), which have especially promoted understanding the British Lower Tertiaries and their relation to those of the Continent, have proved indispensable to the compilation and interpretation of the stratigraphical ranges of the Upper Bracklesham species.

Taxonomic distinctions between the Upper Bracklesham species are in general clear ; generic relationships are in some cases not so clear. Some of the species are almost exactly intermediate between genera, the more modern representatives of which are separated by definite morphological gaps ; others do not fit properly into any known genus. Still another source of difficulty is the confusion arising from mis-application of generic names, as in the case of *Vincularia* Defrance. As a taxonomic expedient, provisional assignment to named genera has been preferred to the institution of new, in most cases monotypical, genera.

The main part of this study was carried out in the British Museum (Natural History) and at Louisiana State University. The biometrical analyses were completed at the University of Stockholm.

I am grateful to the Keeper of Zoology, British Museum (Natural History), for the use of research facilities and specimens in his care ; to the Keeper of Palaeontology for permission to continue working with the Curry Collection after my return to Louisiana State University, as well as to examine other specimens, including the H. Milne Edwards, J. W. Gregory, and A. G. Davis Collections, in his care ; to the

Geology Department, Louisiana State University, for use of research facilities and for financial support for illustrations ; and to the Geological Institute, the University of Stockholm, for the use of research facilities.

Dr. Anna B. Hastings and Dr. H. Dighton Thomas have been extraordinarily generous in guiding me through the many problems—taxonomic, nomenclatorial, and phylogenetic—which have arisen during the course of the study. It is impossible to express strongly enough my warm appreciation of their help and encouragement. Miss P. L. Cook has also given valuable advice on taxonomic problems as well as help in locating specimens and references. Others of the British Museum (Natural History) staff, including Miss S. A. Clark, Mr. R. F. Wise, and Mr. P. J. Hayward, have rendered competent technical assistance for which I am very grateful.

Mrs. Martha M. Deboo, formerly of Louisiana State University, prepared the illustrations. Her assistance has contributed greatly and essentially to the completion of this work.

Mr. Dennis Curry has generously supplied additional material from the Upper Bracklesham Beds at Selsey and samples of the Barton Beds at Barton, Hants, and of the Sables de Fresville (Lutetian) at Gourbesville (Manche), France, from which specimens of Polyzoa were obtained for important comparisons. Dr. Sten Schager of the University of Stockholm provided Rumanian Eocene material which has proved equally important for comparisons.

The National Science Foundation, U.S.A. (through a post-doctoral fellowship in 1961–62), Louisiana State University, and the Chancellor of the Swedish Universities (through a visiting professorship in 1964–65) have all made this research possible.

II. STRATIGRAPHY AND PALAEOGEOGRAPHY

The Curry Collection of Polyzoa was made from the well-known outcrop of the Bracklesham Beds in Bracklesham Bay, at Selsey, Sussex (National Grid, SZ 845926 ; Curry 1958*b* : 34). The exposures, on the foreshore, " are not so good as once they were and so much depends upon the chances of wind and tide that further detailed collecting there requires the complete leisure of a local resident " (Wrigley 1934 : 1).

Though the Bracklesham Beds at Selsey had been studied earlier by Dixon (1850), Fisher (1862) was the first to record the details of their stratigraphy. At Bracklesham Bay, Sussex, and at Whitecliff Bay, Isle of Wight, he recognized four fossil zones (A–D) which comprise alternating beds of glauconitic, shelly sand and sandy clay, " the clays being more prevalent in the highest member, and sands in the lower " (Fisher 1862 : 67). The three lower divisions (B–D) have since been assigned to the Lutetian and Cuisian Stages of the Continental Eocene on the evidence of their larger Foraminifera, *Nummulites laevigatus* (Bruguière) and *N. planulatus* (Lamarck) (see Wrigley & Davis 1937, Curry 1958*a*, 1958*b*, 1962 MS.). The upper division has generally been regarded as Auversian (= Ledian = Lower Bartonian), owing to the occurrence in it of *Nummulites variolarius* (Lamarck), though there is other faunal evidence of its possibly closer affinity to the underlying Lutetian Stage (Curry 1962 MS.).

The Upper Bracklesham Beds, Fisher's division A or the *N. variolarius* zone, has four principal fossil beds (a–d, Fisher 1862 : 67), of which the lower three (b–d) are represented in the exposure in Bracklesham Bay (Fisher 1862 : 74 ; Curry 1958*a*). The Polyzoan collection on which the present work is based came from (c), the highest bed but one, known as the Hard Bed or Fisher Bed 21, after the numbering scheme in Fisher's detailed section. This bed consists of " hard calcareous sand, with comminuted shelly matter and numerous *Tellinae* and other fossils " (Fisher 1862 : 74) ; it is overlain by a softer, clayey sand (b), rich in micro-fossils, termed the Clibs, and is underlain by clays, the *Beloptera* Bed and the *Cypraea* Bed (d), in descending order. The Hard Bed and the *Beloptera* Bed together constitute the Medmery Bed and with the overlying Clibs aggregate some 10 feet thick at Bracklesham Bay (Curry 1958*b* : 34). This group of beds occurs about half way up the Upper Bracklesham sequence and is of similar stratigraphical position to the *Tellina* and *N. variolarius* Beds of Whitecliff Bay, Isle of Wight (Curry 1958*b* : 34).

In contrast to the Polyzoa of the Lower Bracklesham Beds, which are predominantly encrusting forms (membraniporiform) adherent to the exteriors, and especially the interiors, of large molluscan shells, such as *Venericor*, *Clavilithes*, and *Sycostoma* (Davis 1934 : 205), the Cheilostomata of the Upper Bracklesham Beds include only a minority of encrusting types. Erect, arborescent (eschariform) and hollow, globular or discoidal (orbituliporiform ; see Morphology section below) zoaria occur in the greatest numbers ; erect, jointed (cellariiform) and membraniporiform zoaria are only slightly less frequent ; free, discoidal (lunulitiform) specimens are present in smaller numbers ; and fenestrate (reteporiform) zoaria are represented by only a few fragments (see Table I for the zoarial form and abundance of the species). The character of the Upper Bracklesham Cheilostomata, including both the excess of eschariform over membraniporiform zoaria and the relatively large diversity of species and genera, suggests accumulation in deeper, less turbulent water than that in which the Lower Bracklesham fauna lived (Davis 1934 : 205). The significant numbers of lunulitiform specimens attest to the granularity of the substrate, which was composed of shell fragments and Nummulitid and other larger foraminifers, as well as terrigenous detritus. Taken together, these data point to a biotope near the lower limit of effective wave action, perhaps at mid-sub-littoral depths, that is to say, 30–50 fathoms. The large cellariiform component could represent an epi-planktonic fauna essentially independent of bottom conditions. The growth requirements of the orbituliporiform species, making up so large a proportion of the Upper Bracklesham fauna, are, unfortunately, unknown ; however, Lagaaij (1963 : 203–207) has presented convincing arguments that *Fedora nodosa* Silén, a Recent species with somewhat similar growth form, is attached, at least initially, to small lumps of mud on the substrate in deep water (see Morphology section below).

The geographical connexions of the Upper Bracklesham Cheilostomata are more strongly Tethyan than those of any other division of the British Tertiary : 26 of the 38 species occur at least as far south-east as the Paris Basin (see Table II), whereas only 15 of the 29 Lower Bracklesham species and an even smaller proportion of the London Clay and Barton species do. Indeed, several of the Upper Bracklesham species, e.g. *Escharina procumbens* (Canu), *Hippopleurifera canui* nom. nov., and

TABLE I.—Zoarial form and abundance of Upper Bracklesham Cheilostomata

	O	E	C	L	M	R	T
1. *Orbitulipora petiolus* (Lonsdale)	149	—	—	—	—	—	149
2. *Schizostomella curryi* sp. nov.	—	109	—	—	—	—	109
3. *Vincularia monstruosa* (Canu)	—	—	94	—	—	—	94
4. *Lunulites transiens* Gregory	—	—	—	59	—	—	59
5. *Smittoidea variabilis* (Canu)	—	9	—	—	42	—	51
6. *Adeonellopsis punctata* (Canu)	—	45	—	—	—	—	45
7. *Entomaria dutempleana* (d'Orbigny)	—	43*	—	—	43*	—	43
8. *Setosellina gregoryi* sp. nov.	—	—	—	29*	29*	—	29
9. *Batopora glandiformis* (Gregory)	27	—	—	—	—	—	27
10. *Caberoides corniculatus* sp. nov.	—	—	27	—	—	—	27
11. *Escharoides aliferus* (Reuss)	—	24	—	—	—	—	24
12. *Teichopora clavata* Gregory	—	19	—	—	—	—	19
13. *Onychocella subpyriformis* (d'Archiac)	—	—	—	—	19	—	19
14. *Microporina magnipora* (Canu)	—	—	—	—	17	—	17
15. *Vincularia davisi* sp. nov.	—	—	15	—	—	—	15
16. *Celleporina thomasi* sp. nov.	—	—	—	—	12	—	12
17. *Tubucella mamillaris* (Milne Edwards)	—	9	—	—	—	—	9
18. *Sertella marginata* (Reuss)	—	—	—	—	—	9	9
19. *Schizostomella liancourti* (Canu)	—	7	—	—	—	—	7
20. *Nellia tenella* (Lamarck)	—	—	6	—	—	—	6
21. *Gaudryanella variabilis* Canu	—	6	—	—	—	—	6
22. *Labioporella? dartevellei* sp. nov.	—	6	—	—	—	—	6
23. *Cribrilaria parisiensis* (Canu)	—	—	—	—	5	—	5
24. *Membraniporella radiata* (Reuss)	—	4	—	—	—	—	4
25. *Escharella selseyensis* sp. nov.	—	—	—	—	4	—	4
26. *Ogivalina? dimorpha* (Canu)	—	3*	—	—	3*	—	3
27. *Kionidella hastingsae* sp. nov.	2	—	—	—	—	—	2
28. *Schizomavella trigonostoma* sp. nov.	—	2	—	—	—	—	2
29. *Poricellaria alata* d'Orbigny	—	—	2	—	—	—	2
30. *Escharina procumbens* (Canu)	—	2	—	—	—	—	2
31. *Hippoporina globulosa* (d'Orbigny)	—	—	—	—	2	—	2
32. *Adeonellopsis selseyensis* sp. nov.	—	1	—	—	—	—	1
33. *Dakaria beyrichi* (Stoliczka)	—	1	—	—	—	—	1
34. *Setosella fragilis* Canu	—	1	—	—	—	—	1
35. *Smittipora?* sp.	—	1	—	—	—	—	1
36. *Nellia ventricosa* (Canu)	—	—	1	—	—	—	1
37. *Exechonella* sp.	—	—	—	—	1	—	1
38. *Hippopleurifera canui* nom. nov.	—	—	—	—	1	—	1
TOTAL	178	246	145	59	103	9	815
		292*		88*	178*		

* Zoarial form uncertain. Abundance = number of zoaria and zoarial fragments. O = orbituliporiform ; E = eschariform ; C = cellariiform ; L = lunulitiform ; M = membraniporiform ; R = reteporiform ; T = total.

Nellia ventricosa (Canu), have not hitherto been reported north of the Aquitaine region of France. Most of the genera to which the Upper Bracklesham Cheilostomata belong, e.g. *Adeonellopsis* MacGillivray, *Dakaria* Jullien, *Escharina* Milne Edwards, *Escharoides* Milne Edwards, *Hippopleurifera* Canu & Bassler, *Sertella* Jullien, and

Smittoidea Osburn, to-day have rather wide latitudinal ranges but optima in the tropics or sub-tropics ; several, e.g. *Labioporella* Harmer, *Poricellaria* d'Orbigny, and *Setosellina* Calvet, are more distinctly tropical or sub-tropical ; and only a few, e.g. *Escharella* Gray and *Microporina* Levinsen, are more distinctly cool-water. The prevalence of warm-water genera seems, too, to be greater in the Upper Bracklesham fauna than in any other British Tertiary assemblage of Cheilostomata.

TABLE II.—Distribution of Upper Bracklesham Cheilostomata

	Pre-Ypres.	Ypres.	Lutet.	Auvers.	Bart.	Post-Bart.
1. *Ogivalina? dimorpha*	?Pal.	P	P, A	P	—	?Lud.
2. *Poricellaria alata*	?Pal.	—	P, A	E	—	Lud.
3. *Teichopora clavata*		P	P	E, ?B, P	E	
4. *Dakaria beyrichi*		P	P	B	—	Olig.
5. *Entomaria dutempleana*			B, P, A			
6. *Escharella selseyensis*			P			
7. *Gaudryanella variabilis*			P, A			
8. *Hippopleurifera canui*			A			
9. *Nellia ventricosa*			A			
10. *Schizostomella liancourti*			P			
11. *Setosella fragilis*			P			
12. *Escharina procumbens*			A	?A		
13. *Hippoporina globulosa*			P	B, P		
14. *Labioporella? dartevellei*			P	?B		
15. *Vincularia monstruosa*			P, A	?E		
16. *Adeonellopsis punctata*			P, A	—	—	?Lud.
17. *Escharoides aliferus*			P, A	—	—	Lud.
18. *Microporina magnipora*			A	—	—	?Lud.
19. *Onychocella subpyriformis*			E, P, A	B, P	?E, B	Lud.
20. *Smittoidea variabilis*			E, B, P	B	—	Lud.
21. *Membraniporella radiata*			P	B	—	Lud.
22. *Tubucella mamillaris*			B, P, A	B, P	—	Mio.
23. *Nellia tenella*			E, P, A	—	—	Rec.
24. *Lunulites transiens*				E	E	
25. *Setosellina gregoryi*				E, P	E, P	
26. *Orbitulipora petiolus*				E, B, P	B	Olig.
27. *Cribrilaria parisiensis*				B, P	B	Olig.
28. *Batopora glandiformis*					E	
29. *Sertella marginata*						Olig.
30. *Adeonellopsis selseyensis*	KNOWN ONLY FROM THE UPPER BRACKLESHAM BEDS					
31. *Caberoides corniculatus*						
32. *Celleporina thomasi*						
33. *Exechonella* sp.						
34. *Kionidella hastingsae*						
35. *Schizomavella trigonostoma*						
36. *Schizostomella curryi*						
37. *Smittipora?* sp.						
38. *Vincularia davisi*						

E = England ; B = Belgium ; P = Paris Basin ; A = Aquitaine region. Pal. = Palaeocene ; Lud. = Ludian ; Olig. = Oligocene ; Mio. = Miocene ; Rec. = Recent.

Stratigraphically, the Upper Bracklesham species compare most closely with the Lutetian fauna of the Continent: 25 of the 38 species have been recorded no lower than that stage, and six species no higher. Resemblance to the British Lutetian is much less: only three species, *Nellia tenella* (Lamarck), *Onychocella subpyriformis* (d'Archiac), and *Smittoidea variabilis* (Canu), are common to the Upper and Lower Brackleshams (cf. Davis 1934 : 208). Resemblance to Lower Eocene faunas—those of the London Clay and the Continental Ypresian—is lower still. Six species, *Batopora glandiformis* (Gregory), *Cribrilaria parisiensis* (Canu), *Lunulites transiens* Gregory, *Orbitulipora petiolus* (Lonsdale), *Sertella marginata* (Reuss), and *Setosellina gregoryi* sp. nov., are restricted to Auversian and higher units. A total of nine species is so far known only from the Upper Bracklesham Beds.

Despite their considerable resemblance to the French Lutetian fauna, the Upper Bracklesham Cheilostomata seem more likely to represent a late migrant, relict fauna related by descent to the strongly Tethys-influenced Parisian Middle Eocene fauna. Not only are six of the Upper Bracklesham species Auversian and younger guides as mentioned above, but also several of them are direct descendants of Continental Lutetian species: *Lunulites transiens* from *L. urceolata* Lamarck, *Caberoides corniculatus* from *C. canaliculatus* Canu, and *Kionidella hastingsae* from *K. obliqueseriata* Koschinsky. The origins of the Upper Bracklesham Cheilostomata have been traced as far as Senegal where Gorodiski & Balavoine (1962) encountered four of the species—*Nellia tenella*, *N. ventricosa*, *Labioporella*? *dartevellei* and *Ogivalina*? *dimorpha*—in rocks of Palaeocene to Lutetian age. The character of the Upper Bracklesham fauna thus seems to have an important bearing on the palaeogeographical relations between the London–Hampshire Basins and the Tethyan and boreal regions.

Davis & Elliott (1957) adduced evidence that the London and Hampshire Basins were on the south-west margin of an extensive north-west European sea in Ypresian times and that, as the sea transgressed over Belgium and into England from the north-east, it brought a boreal marine fauna into juxtaposition with a tropical terrestrial flora. As a result, both the shoal-water, sandy London Clay (in places with pebble beds) of the Hampshire Basin and the deeper-water London Clay of the London Basin contain a mixture of drifted tropical plant remains with molluscan shells belonging to such boreal genera as *Cyprina*, *Astarte*, *Pholadomya* and *Aporrhais* (Davis & Elliott 1957). At the close of London Clay deposition, the sea regressed eastwards spreading the "Lower Bagshot Sands" across the Hampshire Basin (Davis & Elliott 1957, Curry 1962 MS.).

The next transgressive phase, which began in the Cuisian and probably continued through the Lutetian and Auversian, resulted in prevalence of marine conditions in the Hampshire Basin where the Bracklesham Beds were deposited while the London Basin received sediments (the Bagshot Beds) which are at least in part deltaic (Curry 1962 MS.). The extreme western part of the Hampshire Basin, in the area around Bournemouth, retained non-marine conditions until Bartonian times. These relationships suggest that, whereas the London Clay transgression was essentially an extension of the North Sea, the Bracklesham Beds transgression was mainly, if not entirely, a Tethyan invasion through the Channel. This interpretation seems not out of harmony with the distribution of marine Lutetian, Auversian, and Bartonian deposits in western Europe (see Denizot 1957 : pls. 4, 5). Shoal-water conditions in the Hampshire Basin during the deposition of the Lower Bracklesham Beds may well have prevented the greater number of Tethyan Cheilostomata coming until Auversian times. The Polyzoa from a mid-Channel Tertiary outlier probably of Cuisian or Lutetian age (Curry 1962 : 194) include genera—*Poricellaria*, *Vincularia*, *Lunulites*—of a facies more " Upper Bracklesham " than " Lower Bracklesham " and could thus represent the vanguard of the Selsey fauna.

III. PRESERVATION OF MATERIAL AND TECHNIQUE OF STUDY

The Upper Bracklesham Polyzoa from Selsey are in general very well preserved. Fine tuberculation, striation, and crenulation of the surfaces of many structures have been retained in extraordinary detail (see *Lunulites transiens*, Text-fig. 7 ; *Onychocella subpyriformis*, Text-fig. 10 ; *Entomaria dutempleana*, Text-figs. 25–27 ; and *Schizostomella curryi*, Text-figs. 67–70). Avicularian cross-bars are usually intact, but oral spines have invariably been broken (e.g. in *Hippopleurifera canui*, Text-fig. 39).

The effect of mechanical abrasion before interment is evident in species such as *Smittipora*? sp. (Text-fig. 12) and *Exechonella* sp. (Text-fig. 38) as well as in a few specimens of species in which the preservation is otherwise good (e.g. *Microporina magnipora*, Text-figs. 13, 14 ; and *Gaudryanella variabilis*, Text-figs. 23, 24).

Orifices, opesiae, avicularia, ovicells, and frontal pores are free of matrix in nearly all specimens studied.

Owing to its good preservation and to the very slight adherence of matrix to it, the material required no special preparation beyond the washing it had received before it was presented to the Museum.[1] During the course of their investigation, surface structures such as pits, pores, and striations were put into higher relief by staining the specimens with ordinary, water-soluble, green food-colour. So treated, many otherwise obscure structures became observable under 90 × magnification with a stereo-microscope in reflected light.

All the specimens were mounted on glass- or celluloid-covered, cardboard, microscope slides with gum-tragacanth.

Illustrations were prepared with a camera-lucida attachment on the stereo-microscope at 90 × magnification. Measurements were made on the specimens, rather than on the drawings (see Morphology section below for dimensions measured).

IV. REPOSITORIES FOR MATERIAL

British Museum (Natural History)

All the specimens in the Curry Collection have been retained in the Department of Palaeontology, where each has been given a number bearing the prefix " D ". The holotypes of new species and all the specimens figured in this work, whether they are primary types or not, have been drawn from the Curry Collection.

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[1] Because the Tertiary formations exposed on the foreshore at Selsey are saturated with salt water, material collected from them requires several thorough rinses in fresh water to prevent deterioration of the fossils (Curry 1958*a*).

Geology Museum, Louisiana State University

Where possible, non-figured paratypes of the new species have been obtained from the additional Upper Bracklesham material given to me by Mr. Curry and have been deposited in the Geology Museum, Louisiana State University. These specimens, assigned numbers prefixed " L.S.U.", have been included in the abundance data shown in Table I.

V. MORPHOLOGY OF UPPER BRACKLESHAM CHEILOSTOMATA

Zoarial Characters

Growth habits of Cheilostomata have been analysed in detail by Stach (1936, 1937). To Stach's basic zoarial categories, Brown (1952 : 19, 32–35) added a number of forms which are fundamentally variations on the major growth themes. The main outlines of the Stach–Brown classification are followed here with few modifications.

Membraniporiform, lunulitiform, cellariiform, eschariform, and *reteporiform* patterns, for the most part, are recognizable in the Upper Bracklesham species. Owing to the fragmentary condition of most of the specimens, however, it is not always possible to distinguish between : (1) membraniporiform zoaria which have become detached from their substrate and eschariform zoaria which are unilaminar (either originally or by separation of bilaminar zoaria along discrete basal walls), or (2) cellariiform zoaria which have lost their articulating ends and eschariform zoaria with cylindrical (" vinculariiform ") branches. Some species, e.g. *Smittoidea variabilis,* include two growth forms, even in the same zoarium ; attendant variations in shape, size, and, to some extent, structure of zooecia can be a source of confusion in species determination (Text-figs. 42–46). There is also in some species gradation between zoarial forms resulting from small differences in substratal or other factors in the micro-habitat ; in *Setosellina gregoryi,* for example, the zoarium is alternatively membraniporiform or lunulitiform depending upon whether it started on a large or a small piece of shell or other detritus. In most of the species, however, the zoarial form is not so variable.

The *celleporiform* habit, essentially a variation of the membraniporiform one, seems not to be developed in Upper Bracklesham Cheilostomata with the possible exception of *Hippoporina globulosa* of which there are only two small fragments in the Curry Collection.

It is not possible in the Upper Bracklesham species to discriminate *vinculariiform*[1] and *adeoniform* zoaria from eschariform ones. In *Tubucella mamillaris,* for example, the zoarium begins from an encrusting base as a cylindrical (" vinculariiform ") stem, which, as it rises, soon gives way to lobate, flabellate (adeoniform) fronds, which, in turn, finally become broad and compressed (eschariform) branches (Text-fig. 62). Many of the Upper Bracklesham species, e.g. *Adeonellopsis punctata, Schizostomella curryi,* and *Smittoidea variabilis,* have this robust, dominating growth pattern, here characterized as eschariform.

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[1] The term is an unfortunate one, as the genus *Vincularia* invariably displays the cellariiform habit.

Three species, *Orbitulipora petiolus*, *Batopora glandiformis*, and *Kionidella hastingsae*, assume a colonial growth form different from any heretofore characterized by the terms listed above and for which the name *orbituliporiform* is here proposed. The zoarium in all three species has a distinctive axial hollow round which the erect, prismatic zooecia are grouped in one or more layers. Unlike the similar hollow in *Conescharellina* d'Orbigny, that of the three species mentioned is devoid of tubules presumably derived from heterozooecia (see Silén 1947 : 33). In *Kionidella* the hollow extends nearly the full length of the unilaminar zoarium, its blind (proximal) end formed by the basal wall of the ancestrula and its open (distal) end formed by the basal walls of the most distal circlet of zooecia (Koschinsky 1885 : pl. 7, figs. 5–10). In *Batopora* the hollow runs only part way up the axis of the multilaminar zoarium whose ancestrular region is apparently obscured by superposed zooecia ; the distal end of the hollow is the basal pore surrounded by superposed zooecia (Waters 1919 : 84, pl. 6, figs. 4, 6, 10). In *Orbitulipora* the hollow is restricted to the basal peduncle of the zoarium, round the upper end of which the zoarium expands in a compressed bilaminar frond (Text-fig. 80 ; Canu & Bassler 1931 : pl. 3, figs. 1–22). According to Canu & Bassler (1931 : 17), the ancestrula lies at the upper end of the peduncular tube. The frond of *Orbitulipora* may be either flabellate, with all growth distal from the smaller zooecia, or circular, with growth radial from the smaller zooecia which thus become central. *Orbitulipora* and *Batopora* have the distal ends of the zooecia oriented towards the proximal end of the zoarium as in *Conescharellina*, whereas *Kionidella* has the distal ends of the zooecia directed distally as in typical Cheilostomata.

The mode of growth and the conditions for life of these and other orbituliporiform genera have not been established. Canu (1931 : 144–147) and Canu & Bassler (1931 : 19–21) supposed *Orbitulipora* to be free-swimming, the basal peduncle somehow lending locomotive force by a hydraulic process (presumably like that in the Cephalopoda?). Silén (1947 : 9) stated, concerning a somewhat similar mode of life in *Conescharellina* conjectured by Canu & Bassler (1929*b* : 482, 498), " It must be emphasized that this represents entirely an assumption by these authors and that nobody has ever observed such a phenomenon. Nevertheless the mentioned authors describe the movements of these zoaria in very vivid terms as if they had actually witnessed them." *Conescharellina* either rests upon its flat base on the substrate (and is, thus, lunulitiform) or, more probably, is suspended by chitinous tubes from floating objects (Silén 1947 : 13). On the other hand, the orbituliporiform zoaria of *Kionidella*, *Batopora*, and *Orbitulipora* and the similar ones of *Fedora nodosa* Silén and *F. edwardsi* Jullien (Silén 1947 : 53–55), with their unfilled axial cavities could result from " colonial growth taking place on and around small lumps of hardened mud, which would explain the irregular shape of the cavity " (Lagaaij 1963 : 203, 204). The chitinous tubes which frequently occupy the axial hollows of *Fedora nodosa*, supposed by Silén (1947 : 13) to be connexions between the globular zoaria of that species (which Silén argued were the internodes of a cellariiform zoarium), have proved to be the perisarcs of an associated Hydroid (Lagaaij 1963 : 204–206).

Zooecial Characters

The Upper Bracklesham Cheilostomata occupy such a broad band on the taxonomic spectrum—only four genera, *Nellia*, *Vincularia*, *Schizostomella*, and *Adeonellopsis*, are represented by more than one species, and no genus by more than two—that their zooecial morphology is extremely diverse. Thus, it is not possible to make generalizations about zooecial characters which would apply to the whole assemblage, and the remarks that follow are intended only as amplifications of certain points in the more exhaustive treatments of zooecial morphology contained in the works of Harmer (1926, 1957), Brown (1952), Larwood (1962) and others.

ZOOECIAL WALLS. Basal, lateral, distal, and proximal walls, communication pores, and pore chambers are visible in some of the Upper Bracklesham specimens and are described where observed.

Walls associated with the frontal surface—including sub-frontal cryptocysts and frontal gymnocysts in the Anasca, super-frontal shields in the Acanthostega, and frontal walls in the Ascophora—are of first order significance in the classification of Cheilostomata and are described in as much detail in this work as the material permits. Descriptive terminology (e.g. perforate, marginally areolate) is preferred to a genetical one (e.g. tremocyst, pleurocyst).

ORAL STRUCTURE. In fossil Cheilostomata the structure of the primary orifice is discernible only in the Acanthostega and Ascophora; in the Anasca the orifice is lost during decomposition of the membranous frontal wall, though its form is indicated approximately by the size and shape of the opesia in species having an extensive cryptocyst, especially those belonging to the Microporidae, Poricellariidae, and related families. In the Ascophora the form of the primary orifice, which may be difficult to observe because of the development round it of a peristome with a secondary orifice usually more variable in form, is of paramount importance in classification at the generic level. In the Acanthostega " the shape of the primary orifice is not usually of diagnostic value " (Larwood 1962 : 35). In the present work, oral structure is described by referring to components (e.g. sinus, condyles) rather than to shape designations (e.g. hippoporine, cribriline) which are subject to personal interpretation.

AVICULARIA AND VIBRACULA. A variety of these structures is present in the Upper Bracklesham species : adventitious and vicarious avicularia and interzooecial vibracula (see Larwood 1962 : 41, for definitions of these terms). Vicarious avicularia are certainly more common than adventitious ones in the Anasca and vice versa in the Acanthostega and Ascophora, but exceptions to the general rule occur among the Poricellariidae and Farciminariidae in the Anasca and among the Adeonidae in the Ascophora. The vibraculum-bearing species are Anascans which belong to closely related families, Selenariidae and Lunulitidae.

In most of the Upper Bracklesham species, the avicularia or vibracula, whether adventitious, interzooecial, or vicarious, are well differentiated in form and structure from the normal zooecia. The avicularia often have pointed rostra and pivotal condyles or cross-bars. As noted by Larwood (1962 : 41) the absence of pointed rostra or pivotal structures in fossils may be due to wear; thus it is necessary to examine many specimens before it can be concluded that a species is characterized by avicularia with rounded rostra or without cross-bars. Most of the Upper Bracklesham material is so well preserved, however, that details of avicularian structure can be ascertained from even a few zooecia (see, e.g. *Hippopleurifera canui*, Text-fig. 39; *Escharina procumbens*, Text-figs. 56, 57). In some major taxa, e.g. the Ascophoran family Adeonidae, avicularia are regularly without condyles or cross-bar, but Brown's (1952 : 191) suggestion that adventitious avicularia in the Anasca are always without such structures is incorrect (see Harmer 1926 : pl. 14, figs. 18–20, *Nellia tenella*; pl. 23, figs. 6–8, *Poricellaria ratoniensis*).

In four species of Upper Bracklesham Cheilostomata, belonging to widely separated families, vicarious avicularia[2] are only feebly differentiated from the normal zooecia. The differentiation is least in *Labioporella*? *dartevellei* (Text-figs. 21, 22) where it consists in slight enlargement of the avicularian (?) zooecia. In the two species of *Vincularia*, *V. monstruosa* (Text-figs. 30, 31) and *V. davisi* (Text-figs. 33, 34), the avicularian (?) zooecia have undergone curvature on their proximo-distal axis in addition to slight enlargement. The avicularian zooecia of *Schizostomella curryi* (Text-figs. 68, 70) are enlarged in the oral region in just the same way as the avicularia (= B-zooecia) are in *Steganoporella* (see Harmer 1926 : 268).

Ovicells and gonoecia. The systematic importance of the ovicell, one of the basic tenets upon which Canu & Bassler (1917, 1920, 1927, 1929*b*) established their classification of the Cheilostomata, has been seriously questioned by Silén (1944), Brown (1952), Lagaaij (1952) and Larwood (1962). The separation of five morphological types—hyperstomial, entozooecial, peristomial, vestibular, and entotoichal (Brown 1952 : 36, 37)—is still a useful descriptive device in spite of the large amount of mutual inter-gradation.

Hyperstomial ovicells are the most common type in the Upper Bracklesham Cheilostomata: 14 of the 38 species display them. Entozooecial ovicells occur in three species, and peristomial ovicells in one. None displays vestibular or entotoichal ovicells, though Canu (1925 : 47) described the ovicell of *Entomaria dutempleana* as entotoichal evidently through mis-interpretation (see Systematics section below and Text-fig. 27).

Five species, all belonging to the family Adeonidae, possess specially modified zooecia (gonoecia = gonozooecia of Brown 1952 : 37, not Cheetham 1962) instead of ovicelled zooecia. The gonoecia show a progressive series of modifications in the Upper Bracklesham Adeonidae from the feebly differentiated dimorphs of the ordinary zooecia of *Teichopora clavata* (Text-figs. 65, 66), through the distally swollen, orally modified gonoecia of *Schizostomella curryi* (Text-figs. 67–69) and *Adeonellopsis selseyensis* (Text-fig. 73), to the generally swollen, orally and frontally modified gonoecia of *Adeonellopsis punctata* (Text-figs. 74, 75).

The remaining 15 species of Upper Bracklesham Cheilostomata apparently lack specially modified fertile zooecia of any sort.

[2] It is possible that these features are other forms of zooecial dimorphs in the four species concerned.

Measurements

Certain linear dimensions are usually measured in descriptive work on Cheilostomata (Canu & Bassler 1920, 1923; Osburn 1950, 1952; Brown 1952; Lagaaij 1952; Larwood 1962; Cheetham 1962, 1963*b*). For the Upper Bracklesham species the following are recorded:

Lz = zooecial length, the maximum distance between the zooecial proximal and distal margins projected to the proximo-distal axis of the frontal surface.

lz = zooecial width, the maximum distance between the zooecial lateral margins measured perpendicular to the proximo-distal axis of the frontal surface.

ho = oral or opesial length, measured in the same direction as the proximo-distal axis of the zooecial frontal surface and always in the plane of the orifice or opesia even where that plane is not parallel to the frontal surface.

(For sinuate orifices, oral length includes the sinus.)

lo = oral or opesial width, measured perpendicular to oral or opesial length.

(Oral dimensions are taken at the primary orifice where possible; where measurements of secondary orifice are substituted, a notation to that effect is given in the Measurements section of the species description.)

Lov = ovicell length, the maximum distance between the proximal and distal margins of the ovicell projected to the proximo-distal axis of its frontal surface.

(Ovicell length is determined only for hyperstomial ovicells, owing to the lack of definite margins in entozooecial and peristomial ones. The full length, width, and oral dimensions of gonoecia are recorded for species in which those structures supplant ovicelled zooecia.)

Lav or *Lv* = avicularian or vibracular length, the maximum distance between rostrum and opposite margin measured in the plane of the avicularian or vibracular upper surface.

(Width and oral dimensions are recorded for vicarious avicularia only.)

Zoarial dimensions are recorded for reteporiform and orbituliporiform species only.

The arithmetic mean and standard deviation of each linear dimension of each species are calculated by the standard formulae, and the number of specimens measured and the observed range of the dimension are recorded. For brevity, the following scheme of presentation is used throughout the Systematics part of this paper:

Lz	(10)	0·500	(0·0500) mm.	0·45–0·55 mm.
Character symbol	(Number of specimens)	Mean	(Standard deviation)	Observed range

All dimensions are in decimal fractions of a millimeter, the observed range expressed to the nearest 0·01 mm., and the mean and standard deviation carried, respectively, one and two places farther. Measurements were taken with a 15× micrometer ocular in an American Optical stereo-microscope fitted with 6× objective, and each observation was recorded to the nearest whole micrometer division. Means, standard deviations, and observed ranges are calculated in micrometer units and then converted to millimeters by the factor 0·00855 mm. per micrometer unit.

TAXONOMIC SIGNIFICANCE OF MEASUREMENTS. Assessment of the value of quantitative characters as a discriminatory tool in Cheilostome taxonomy has barely been started by studies of variation in a few species (e.g. the works of Illies 1953 and David & Mongereau 1961). The pessimistic feelings of most workers are probably typified by the remarks of Brown (1952 : 33, 34) that " no great importance is attached to the value of . . . measurements as they are found to vary widely even in the same colony," or that " they are seldom to be used as the basis for differentiating species in the absence of other differences of a more positive character " (see also Larwood 1962 : 45, 46). Lack of evaluation has not kept some authors from founding species chiefly, or even solely (see Canu & Bassler 1919 : 89, *Steganoporella parvicella*), on dimensional criteria. Examples of quantitative discrimination which has subsequently proved erroneous are provided by some of Lang's Cretaceous Cribrimorphs (revised by Larwood 1962) and some of Canu & Bassler's Tertiary species of *Steganoporella* (revised by Cheetham 1963*b*).

Knowledge of the magnitude of variability is crucial to the assessment of any dimensional character as a taxonomic criterion. Yet most authors who have described Cheilostomata have failed to include any meaningful measure of variability in their specific characterizations, despite the fact that they have given some form of measurement. They have generally followed Canu in giving either a single, " typical " value, perhaps obtained as the arithmetic mean of an unstated number of observations, or a range of values obtained as the extremes of an again unstated number of observations. Either alternative gives almost no information about the dispersion of the character in the sample at hand or in the population from which it was drawn (Simpson, Roe & Lewontin 1960 : 78–82).

Variance and standard deviation are certainly the most widely used measures of variability in statistical work. From the standard deviation may be calculated, not only the standard error from which confidence limits for the population mean may be obtained, but also, a measure of relative variability, Pearson's coefficient of variation, from the formula

$$V = \frac{100s}{\bar{x}}.$$

By use of V's so obtained, it is possible to compare variation of a character in different samples of the same species or in different species (Simpson, Roe & Lewontin 1960 : 90).

For the Upper Bracklesham species, it is necessary to correct the V's, because of small sample size, by Haldane's method (Simpson, Roe & Lewontin 1960 : 101, 102) :

$$V_c = \frac{V(4N + 1)}{4N}.$$

The values of V_c for the Upper Bracklesham species are presented in Table III.

TABLE III.—Corrected coefficients of variability of linear dimensions of Upper Bracklesham Cheilostomata

	Lz	lz	ho	lo	Lov	Lav or Lv
1. *Ogivalina? dimorpha*	13·9	23·2	17·0	16·5	—	—
2. *Setosellina gregoryi*	9·5	12·7	10·2	12·5	—	10·4
3. *Lunulites transiens*	8·2	4·5	13·4	9·8	—	18·9
4. *Onychocella subpyriformis*	15·8	10·5	10·2	11·4	—	6·3
5. *Smittipora?* sp.	11·7	6·4	11·9	14·9	—	—
6. *Microporina magnipora*	6·2	12·8	4·4	5·8	—	—
7. *Setosella fragilis*	2·9	7·9	7·4	11·1	—	—
8. *Poricellaria alata*	6·4	9·4	13·2	0·0	—	18·2
9. *Labioporella? dartevellei*	5·6	11·8	9·8	22·2	—	—
10. *Gaudryanella varibilis*	9·7	13·7	10·0	14·8	—	—
11. *Entomaria dutempleana*	12·9	10·0	23·0	9·9	—	22·2
12. *Nellia tenella*	4·2	10·8	10·5	12·2	—	23·0
13. *Nellia ventricosa*	4·1	17·8	5·2	25·1	—	10·2
14. *Vincularia monstruosa*	8·2	10·9	9·8	6·7	—	a 23·4 6·8
15. *Vincularia davisi*	8·9	6·3	3·3	10·7	—	6·8
16. *Cribrilaria parisiensis*	6·0	13·2	10·8	7·9	5·2	12·8
17. *Membraniporella radiata*	4·3	15·0	10·0	13·2	6·3	5·2
18. *Exechonella* sp.	4·0	6·8	12·3	10·4	—	—
19. *Hippopleurifera canui*	3·3	3·4	6·1	12·7	—	—
20. *Escharoides aliferus*	12·0	12·1	14·3	4·5	10·6	22·3
21. *Smittoidea variabilis*	b 15·2 17·0	12·5 20·8	10·4	9·1	7·8 8·7	17·8
22. *Escharella selseyensis*	15·9	14·8	13·6	4·9	6·2	—
23. *Sertella marginata*	6·6	6·7	18·4	13·6	9·2	c 21·6 8·3 17·3 17·7
24. *Dakaria beyrichi*	6·8	14·4	19·6	7·4	—	—
25. *Schizomavella trigonostoma*	12·8	26·8	13·0	5·2	—	15·6
26. *Escharina procumbens*	10·8	23·2	8·5	9·3	0·0	12·0
27. *Hippoporina globulosa*	17·0	13·4	7·3	4·6	3·6	3·0
28. *Caberoides corniculatus*	6·6	10·9	10·4	7·6	1·5	7·0
29. *Tubucella mamillaris*	9·9	13·2	15·1	18·5	—	—
30. *Teichopora clavata*	3·3	5·5	9·1	12·7	5·2	d 12·9 13·1
31. *Schizostomella curryi*	9·1	3·1	11·5	12·5	3·6	d 22·4 16·1
32. *Schizostomella liancourti*	12·1	15·9	19·8	12·1	—	17·6
33. *Adeonellopsis selseyensis*	9·9	6·7	8·8	6·0	3·3	9·0
34. *Adeonellopsis punctata*	13·9	9·6	12·7	7·9	7·1	18·2
35. *Celleporina thomasi*	13·2	10·4	13·9	5·4	6·6	8·8
36. *Kionidella hastingsae*	20·8	6·5	6·5	8·9	10·8	14·8
37. *Orbitulipora petiolus*	11·3	13·4	20·1	9·5	11·6	—
38. *Batopora glandiformis*	18·4	14·3	12·5	19·9	11·4	0·0

[a] Vicarious and adventitious avicularia. [b] Zooecia on uni- and bilaminar fragments. [c] Polymorphic avicularia. [d] Dimorphic avicularia. Lz, lz, ho and lo exclude modified zooecia.

The significance of coefficients of variation can be judged by comparing *V*'s for many species, a procedure which Simpson, Roe & Lewontin (1960 : 90) deemed

" generally valid if the variates are analogous and belong to the same category—for instance, if they are all linear dimensions of anatomical elements ".[3] For mammals, linear dimensions yield " hundreds of V's, . . . the great majority " of which " lie between 4 and 10, and 5 and 6 are good average values " (Simpson, Roe & Lewontin 1960 : 91). By this standard, the Upper Bracklesham Polyzoa are extraordinarily variable. David & Mongereau (1961), in their study of *Cellaria fistulosa* auctt. *non* Linné, obtained variances and means from which V's of 6·9 for zooecial length and 9·0 for zooecial width may be calculated. These are lower than for most of the Upper Bracklesham species, though comparable to the ones for species having cellariiform zoaria.

In order to broaden the comparison of variability of characters, it is possible to include in this analysis two American Early Tertiary assemblages of Cheilostomata (Cheetham 1962, 1963*b*) for which $\bar{x}$, s, and N of standard dimensions have been recorded. V's are calculated and corrected by the same formulae used for the Upper Bracklesham species. Then, for each linear dimension, the number of species in the combined fauna having V_c less than 10·0 is entered in Table IV. These species numbers are expressed as percentages of the total number of species showing the character, and for each percentage approximate 95% confidence limits are calculated by the formula

$$p_{0\cdot 95} = p \pm 2\sqrt{\frac{p(1-p)}{N}}$$

(Sylvester-Bradley 1958 : 222).

The value 10·0 was chosen as the limit between high V's and low ones, not just because Simpson, Roe & Lewontin considered values of 4–10 to be usual, but also because variability amounting to no more than 10% of the mean indicates a relatively small overlap between populations even where the difference between their means is fairly small. For example, if normal distribution of the variate is postulated for each of two populations A and B, 90% of A will be distinct from 90% of B even where the difference between their means ($|\bar{x}_A - \bar{x}_B|$) amounts to no more than 0·128 $(\bar{x}_A + \bar{x}_B)$, provided that their V's are 10 or less and that their variances are approximately equal.[4] Canu & Bassler (1920 : 262, 263), as mentioned above, established two species of *Steganoporella* on a difference in mean zooecial width of this magnitude ($|\bar{x}_A - \bar{x}_B| = 0{\cdot}12$ mm. ; $0{\cdot}128\ (\bar{x}_A + \bar{x}_B) = 0{\cdot}077$ mm.), but, unfortunately, the variation in that character was subsequently shown (Cheetham 1963*b* : 54–56) to be much too great, at $V = 18{\cdot}2$, for specific separation. On the other hand, the difference in mean zooecial lengths of two of the Upper Bracklesham species, *Vincularia monstruosa* and *V. davisi*, at 0·162 mm.,[5] is greater than $0{\cdot}128\ (\bar{x}_A + \bar{x}_B) = 0{\cdot}133$ mm., and both *V*'s are less than 10 ; thus the two species are approximately 90% distinct in this dimension (and, in addition, show other differences " of a more positive character ").

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[3] Reyment (1963 : 684) regarded as valid only comparisons of the same character.

[4] Ninety per cent. joint non-overlap is regarded as the minimum requirement for separate taxonomic status by some systematists (e.g. Mayr, Linsley & Usinger 1953 : 145). However, as Sylvester-Bradley (1958 : 225–227) has pointed out, overlap in several uncorrelated characters taken simultaneously may be less than 10% even where any single one shows overlap of more than 10%.

The expression $0{\cdot}128(\bar{x}_A+\bar{x}_B)$ may be derived from Mayr, Linsley & Usinger's (1953 : 146) coefficient of difference, by substituting $S_A = 0{\cdot}10\bar{x}_A$ and $S_B = 0{\cdot}10\bar{x}_B$.

[5] Even if the nearer limits of their 95% confidence intervals are used, the difference indicates 87·5% non-overlap.

TABLE IV.—Relative variability of linear dimensions of Cheilostomata (Based upon data from the Upper Bracklesham species and from Cheetham 1962, 1963*b*)

	No. Spp.	No. Spp. $V_c <$ 10·0	%	Conf. limits
A. Relatively constant characters:				
1. Length of vicarious avicularium	12	10	83·3	61·7 104·9
2. Width of primary orifice	38	31	81·6	68·0 95·2
3. Length of ovicell or gonoecium	33	24	72·7	57·0 88·4
B. Relatively variable characters :				
1. Length of zooecium	89	48	53·9	43·3 64·5
2. Width of zooecium	88	45	51·1	40·3 61·9
3. Length of primary orifice	38	18	47·4	31·2 63·6
4. Length of opesia not separate from opesiules .	27	12	44·4	25·3 63·5
5. Length of avicularium or vibraculum regardless of position	43	16	37·2	22·5 51·9
6. Width of opesia not separate from opesiules .	27	9	33·3	15·2 51·4
7. Length of adventitious avicularium	30	6	20·0	5·4 34·6
C. Characters for which evidence is insufficient to judge variability :				
1. Length of opesia separate from opesiules . .	8	5	72·7	28·3 96·7
2. Width of opesia separate from opesiules . .	8	4	50·0	14·6 85·4
3. Length of interzooecial vibraculum	4	2	50·0	0·0 100·0
4. Width of secondary orifice	12	5	41·7	13·2 70·2
5. Length of secondary orifice	15	6	40·0	14·7 65·3

It must be emphasized that, in comparisons of the sort exemplified here, " the mean is a necessary statistic but it cannot be used on its own to test assumptions of difference in dimensions. For this one requires a statistic which is able to express the spread of the data " (Reyment 1963 : 684). Therefore, it is of the utmost importance that a measure of variability be attached to all data which are presented in a taxonomic context. The coefficient of variation, though useful in preliminary assessment of single variates of the type illustrated here, is not employed in multivariate analysis.

This first evaluation of linear dimensions in Eocene Cheilostomata, summarized in Table IV, has identified three characters—length of vicarious avicularium, width of primary orifice, and length of ovicell or gonoecium—as relatively less variable than most. As one or more of these are measurable in most species of Cheilostomata, they are potentially useful in discrimination of species and sub-species. Even the comparatively more variable characters, especially zooecial length and width, are sufficiently constant in some species for use as a taxonomic criterion as shown above. Only one dimension, length of adventitious avicularium, seems so variable as to be taxonomically almost useless. How much of the variability in the latter character is due to differential breakage of these vulnerable structures must remain for the present one of the imponderables.

VI. CLASSIFICATION AND GENERAL ARRANGEMENT

The Upper Bracklesham Cheilostomata include representatives of all three sub-orders: Anasca, 15 species; Acanthostega (= Cribrimorpha; see Cheetham 1963*b* : 60), 2 species; and Ascophora, 21 species.

The supra-generic classification of the order is seriously in need of overhaul, but such a project is not within the compass of the present work. Thus no categories between sub-order and family are employed here, and some of the families, e.g. Hincksinidae, are accepted only provisionally. Most of the families used here have been accepted by Harmer (1926, 1934, 1957), but a few, e.g. Selenariidae and Farciminariidae in the Anasca and Ditaxiporinidae in the Ascophora, are not found in his works. The family Labioporellidae Harmer is not deemed sufficiently distinct from the Steganoporellidae for recognition here. I do not follow Harmer (1957 : 824) in suppressing the well-known name Tubucellariidae in favour of the obscure Margarettidae based upon the senior synonym for the type genus.

The scheme of presentation of the systematic sections of this work is similar to those used by Brown (1952) and Larwood (1962).

Families and taxa of higher categories are not defined here as definitions are available in recent literature.

Genera. Only those genera for which new information, including revision or clarification, is presented are diagnosed in this work. For each genus diagnosed, the synonymy (including only the original reference and references to name changes), the type species, the diagnosis, and remarks on nomenclature or taxonomy are given in that order. In the diagnoses, characters are described in approximate order of taxonomic importance: (1) frontal wall and associated structures, (2) oral structures, (3) heterozooecia, (4) ovicells or gonoecia, (5) interzooecial communication, (6) zooecial shape and arrangement, and (7) zoarial form.

Species. Every species studied, including the two left *nomina aperta*, is described. For each, a detailed synonymy is given first, and a list of the material studied, type and non-type, figured and non-figured specimens, next. The species diagnosis and then its description, based on all material available, follow the list of specimens ; some features, e.g. ovicells or avicularia, lacking in the material at hand but described in the literature, are included in the species descriptions by reference to the pertinent literature. Measurements (see Morphology section above for scheme of presentation) and remarks on nomenclature and taxonomy follow the species description. Finally, under distribution is summarized the known stratigraphical and geographical extent of the species as compiled from the literature.

VII. SYSTEMATIC DESCRIPTIONS

Phylum POLYZOA

Class *ECTOPROCTA*

Subclass *GYMNOLAEMATA*

Order CHEILOSTOMATA

Suborder ANASCA

Family **HINCKSINIDAE** Canu & Bassler

Genus ***OGIVALINA*** Canu & Bassler

1917 *Ogivalina* Canu & Bassler : 16.

Type species (by original designation). *Ogivalina eximipora* Canu & Bassler 1917 : 17, pl. 2, fig. 1. Eocene (Jacksonian) ; Castle Hayne Marl, Wilmington, North Carolina, U.S.A.

Diagnosis. Frontal wall membranous, gymnocyst greatly reduced or lacking. Cryptocyst well developed, especially proximally, coarsely granular. Opesia large, oval to sub-circular, without distinct opesiular indentations. Avicularia interzooecial or lacking, not initiating new zooecial rows, with pointed rostra, lacking cryptocyst or pivotal structures. Ovicell entozooecial, inconspicuous. Interzooecial communication by pores without chambers.

Ogivalina? dimorpha (Canu)

(Text-figs. 1–3)

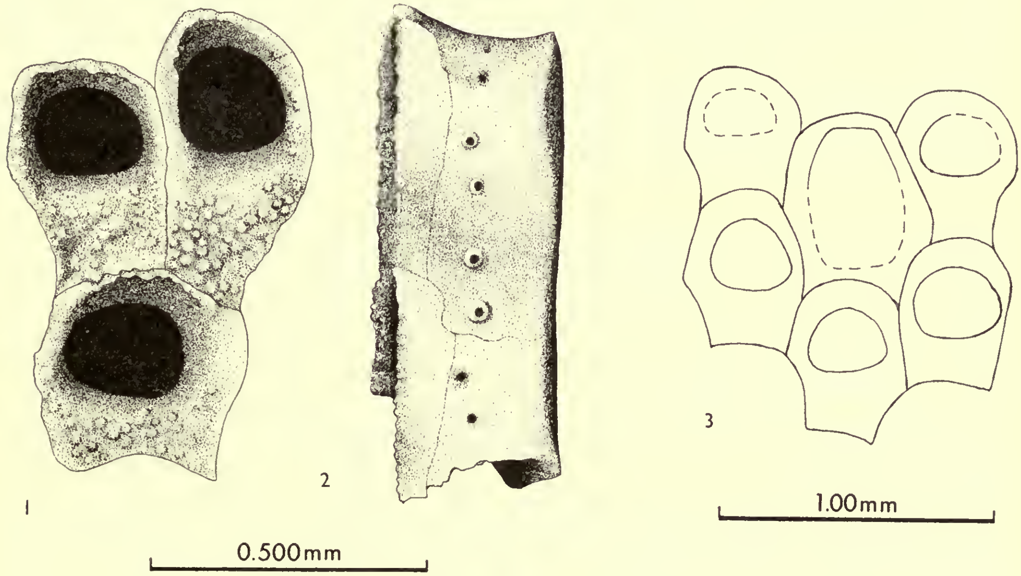
1907*b* *Onychocella dimorpha* Canu : 79, pl. 11, figs. 1–3.
1926 *Onychocella dimorpha* Canu ; Canu : 749, pl. 27, fig. 6.
1933 *Onychocella dimorpha* Canu ; Dartevelle : 106.
1935 *Rectonychocella dimorpha* (Canu) Dartevelle : 112.
1936 *Onychocella dimorpha* Canu ; Dartevelle : 29.
1946 *Stamenocella? dimorpha* (Canu) Buge : 431.
1949 *Onychocella dimorpha* Canu ; Balavoine : 773.
1960 *Stamenocella dimorpha* (Canu) ; Balavoine : 246.
?1962 *Stamenocella dimorpha* (Canu) ; Gorodiski & Balavoine : 5.
?1963 *Vibracella trapezoidea* (Reuss) ; Malecki : 109, pl. 10, fig. 9.

Figured specimens. D.48341 (Text-fig. 1), D.48342 (Text-fig. 2), D.48343 (Text-fig. 3).

Diagnosis. *Ogivalina* (?) with dimorphic zooecia, the ordinary ones with very extensive cryptocyst and transversely elliptical opesia, the " membraniporoid " ones without cryptocyst ; avicularia large, pointed, sometimes initiating zooecial rows.

Description. *Zoarium* encrusting or erect, uni- or bilaminar, the zooecia arranged in easily separable, longitudinal rows ; in bilaminar fragments, the two laminae are easily separable.

Zooecia separated by faint grooves between beaded mural rims, dimorphic : (1) *Ordinary zooecia* claviform, broadly rounded distally, straight sided proximally ; width variable from about half length to just over length ; cryptocyst well developed, imperforate, finely and evenly tuberculate except where worn, relatively flat and little depressed below mural rim, descending slightly towards opesia ; opesia subcircular to elliptical, its major axis transverse, completely rimmed by a smooth collar forming a narrow shelf distally and a steeply descending " oral lamina " (see Canu 1907*b* : 79) proximally. (2) " *Membraniporoid* " *zooecia* rhomboidal, straight sided distally as well as proximally ; width regularly two-thirds length (see Canu 1907*b* : 79) ; cryptocyst lacking ; opesia elliptical, its major axis longitudinal, without distal shelf or proximal " oral lamina ".



Figs. 1–3. Fig. 1. *Ogivalina*? *dimorpha* (Canu). D.48341. Three ordinary zooecia. Fig. 2. *Ogivalina*? *dimorpha* (Canu). D.48342. Two ordinary zooecia in lateral aspect. Fig. 3. *Ogivalina*? *dimorpha* (Canu). D.48343. Outline drawing of five ordinary zooecia and one " membraniporoid " zooecium.

Interzooecial communication by a single row of about 12 simple pores near middle of lateral and distal walls.

Avicularia lacking in material at hand.

Ovicell unknown.

Measurements :

Ordinary zooecia

Lz (10) 0·486 (0·0659) mm., 0·37–0·56 mm.
lz (10) 0·380 (0·0860) mm., 0·26–0·49 mm.
ho (10) 0·216 (0·0358) mm., 0·16–0·26 mm.
lo (10) 0·276 (0·0432) mm., 0·20–0·32 mm.

" Membraniporoid " zooecia

Lz (1) 0·62 mm.
lz (1) 0·44 mm.
ho (1) 0·56 mm.
lo (1) 0·37 mm.

Remarks. The generic position of this distinctive species remains doubtful. It resembles the American Eocene *O. eximipora* Canu & Bassler (1917 : 17, pl. 2, fig. 1 ; 1920 : 118, pl. 23, figs. 6, 7) in the following characters : (1) shape, size, and mode of communication of zooecia ; (2) extent and ornamentation of the cryptocyst ; (3) general shape of opesia and presence of a descending " oral lamina " on its proximal margin ; (4) form and position of avicularia (*fide* Canu 1907*b* : pl. 11, figs. 1–3). The Upper Bracklesham specimens lack avicularia but resemble the French specimens illustrated by Canu in other respects.

Distribution. ?Palaeocene ; Senegal. Eocene (Ypresian, Lutetian, Auversian); France. ?Eocene (Ludian) ; Poland.

Family **SELENARIIDAE** Busk

Genus ***SETOSELLINA*** Calvet

1906 *Setosellina* Calvet : 157.
1917 *Vibracellina* Canu & Bassler : 14.

Type species (by monotypy). *Setosellina roulei* Calvet 1906 : 157. Recent ; Cape Verde Islands.

Diagnosis. Frontal membranous, gymnocyst reduced. Cryptocyst very narrow, not widened proximally. Opesia oval to sub-pyriform, wider proximally, without differentiated opesiular indentations. Vibracula interzooecial, one placed at distal end of each zooecium ; vibracular opesia reniform. Ovicell lacking. Zoarium encrusting, in later stages of growth usually becoming free and discoidal ; zooecial rows originate by spiral growth from ancestrula.

Setosellina gregoryi[6] sp. nov.

(Text-figs. 4–6)

1893 *Biselenaria offa* Gregory : 235 [*partim*—pl. 30, fig. 5 ; *non* pl. 30, figs. 4, 4*a* (=*Orbitulipora petiolus*)].
1907*b* *Biselenaria offa* Gregory ; Canu : 85, pl. 12, figs. 1–3.
1926 *Vibracellina offa* (Gregory) Canu : 747.
1929 *Biselenaria offa* Gregory ; Burton : 348.
1933 *Vibracellina offa* (Gregory) ; Dartevelle : 106, 113.
1936 *Vibracellina offa* (Gregory) ; Dartevelle : 29.
1946 *Biselenaria offa* Gregory ; Buge : 430.

HOLOTYPE. D.48344 (Text-fig. 6).

PARATYPES. D.48346 (Text-fig. 4), D.48345 (Text-fig. 5), D.48347–371 (26 specimens), and L.S.U. 8032.

DIAGNOSIS. *Setosellina* with zoarium free and discoidal in later stages, zooecia arranged in anti-clockwise spirals round small ancestrula ; basal side of zoarium flat or slightly concave, formed of smooth, irregularly radiating sectors ; peripheral ring of large or small vibracula on basal surface.

DESCRIPTION. *Zoarium* unilaminar, encrusting shell fragments or Nummulitids in early stages, becoming free and discoidal in later stages. Zooecia arranged in two repeatedly bifurcating, anti-clockwise, spirally coiled lines, each one emanating from a vibraculum on the lateral margin of the central ancestrula. Basal surface flat or slightly concave, with solid, smooth, irregularly radiating sectors projecting from marginal zooecia back to ancestrular region.

Ancestrula slightly more than half as long as mature zooecia, otherwise of the same form. First two post-ancestrular zooecia slightly larger. Succeeding zooecia all of full size. Ancestrula, and less frequently the two small zooecia, partly closed by a calcareous lamina with a central pore.

Zooecia irregularly oval, separated by deep grooves. Length slightly greater than width. Gymnocyst smooth, convex, narrow, extending entirely round zooecium but developed best proximally and laterally. Mural rim sharp, smooth, not raised. Cryptocyst very narrow, forming a horse-shoe laterally and proximally, descending steeply all round the opesia ; surface finely granular and radially striated. Interzooecial communication by a few simple pores in distal and lateral walls.

Opesia irregularly oval to elliptical, without differentiated opesiular indentations.

Vibracula interzooecial, usually smaller than zooecia, one placed at distal end of each zooecium, except ancestrula which has two lateral vibracula. Vibracular opesia reniform, its main axis an extension of that of its proximal zooecium ; vibracular condyle on right larger than that on left. Vibracula on periphery of basal surface of same form as those on frontal side of zoarium but occasionally greatly enlarged.

Ovicell lacking.

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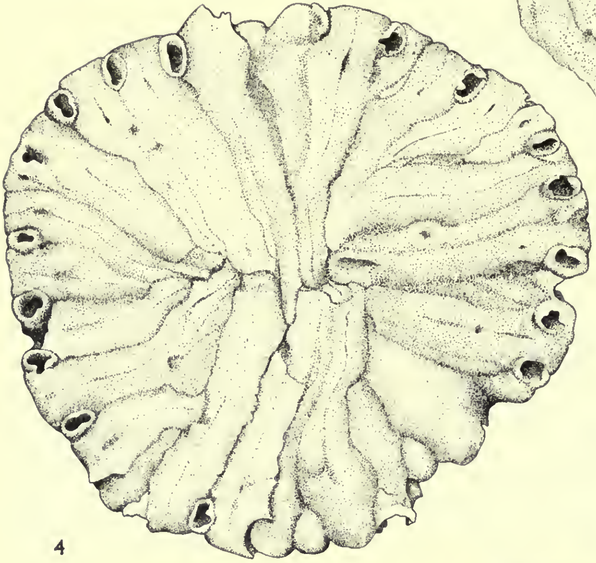
[6] After the late J. W. Gregory.



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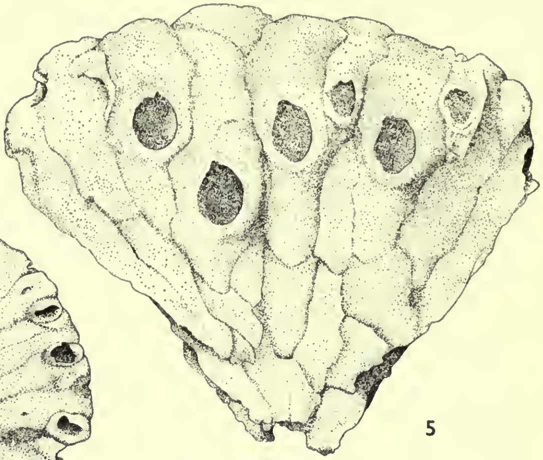

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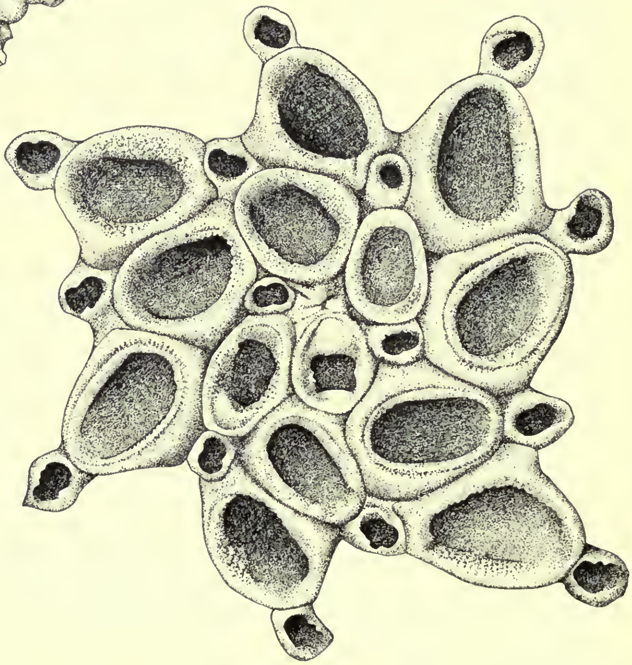

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MEASUREMENTS :

Ancestrula

Lz	(4) 0·180 (0·0121) mm., 0·17–0·20 mm.
lz	(4) 0·143 (0·0117) mm., 0·13–0·15 mm.
ho	(4) 0·132 (0·0049) mm., 0·13–0·14 mm.
lo	(4) 0·081 (0·0110) mm., 0·07–0·09 mm.
Lv	(4) 0·086 (0·0000) mm., 0·09 mm.

Mature zooecia

Lz	(10) 0·302 (0·0280) mm., 0·26–0·36 mm.
lz	(10) 0·250 (0·0310) mm., 0·21–0·30 mm.
ho	(10) 0·211 (0·0210) mm., 0·19–0·26 mm.
lo	(10) 0·129 (0·0158) mm., 0·10–0·16 mm.
Lv	(10) 0·120 (0·0121) mm., 0·10–0·14 mm.

REMARKS. Gregory (1893 : 235) described *Biselenaria offa* from the Barton Beds, Barton, Hants., on the basis of three specimens on slide 49759, Edwards Collection, illustrated on his plate 30 as " Fig. 4. Zoarium of type specimen : upper surface. Fig. 4*a*. Part of another specimen : under surface. Fig. 5. Upper surface of another zoarium." The specimens illustrated on his figs. 4 and 4*a* are conspecific with *Cellepora petiolus* Lonsdale, the type species of *Orbitulipora* (see description of that species below). The third specimen is conspecific with the material referred to by Canu, Burton, Dartevelle and Buge as " *Biselenaria offa* Gregory ". Unfortunately, as Gregory clearly designated as holotype one of the specimens of *Orbitulipora petiolus*, there is no alternative to giving this species a new name.

S. gregoryi is a guide species to Upper Eocene (Auversian and Bartonian) strata on both sides of the Channel. It has its nearest counterpart in the Recent Mediterranean species *S. capriensis* (Waters) in which the zoarium is more conical with a more concave base, the zooecia are larger and arranged in clockwise spirals, and the peripheral vibracula are placed on the edge of the zoarium rather than on the basal surface. *S. goesi* (Silén), a Recent Caribbean and Gulf of Mexico species, encrusts larger grains than the other two species and thus never becomes fully lunulitiform. Lagaaij (1963 : 172) reported both clockwise and anti-clockwise spirals in *S. goesi*. The coincidence of the smaller vibracular condyle and the direction of coiling of the zooecial rows noted by Lagaaij in *S. goesi* is also distinguishable in *S. gregoryi*.

DISTRIBUTION. Eocene (Auversian, Bartonian) ; England, France.

FIGS. 4–6. Fig. 4. *Setosellina gregoryi* sp. nov. D.48346. Paratype. Basal view of a small, nearly complete zoarium. Fig. 5. *Setosellina gregoryi* sp. nov. D.48345. Paratype. Basal view of a larger, fragmentary zoarium. Fig. 6. *Setosellina gregoryi* sp. nov. D.48344. Holotype. Ancestrular region showing zooecia and vibracula.

Family **LUNULITIDAE** Lagaaij

Genus ***LUNULITES*** Lamarck

Lunulites transiens Gregory

(Text-figs. 7–9)

1850 *Lunulites urceolata* Lamarck ; Lonsdale : 159, pl. 1, fig. 8.
1878 *Lunulites urceolata* Lamarck ; Lonsdale : 201, pl. 1, fig. 8.
1893 *Lunulites transiens* Gregory : 233, pl. 29, figs. 13, 14 ; pl. 30, fig. 1.
1933 *Lunulites transiens* Gregory ; Dartevelle : 106, 113.

HOLOTYPE. 49724, Edwards Collection. Barton Clay ; Barton, Hants. Figured by Gregory (1893, pl. 29, fig. 14).

FIGURED SPECIMENS. D.48372 (Text-fig. 7), D.48373 (Text-fig. 8), D.48374 (Text-fig. 9).

ADDITIONAL MATERIAL. Fifty-six specimens, D.48375–D.48430.

DIAGNOSIS. *Lunulites* with discoidal, slightly concavo-convex zoarium, basal surface divided into irregular, finely perforate, radial sectors ; new zooecial rows originating from vibracular rows ; mural rims of adjacent zooecia confluent, forming thick, high transverse ridge between zooecia of same row ; cryptocyst very narrow, shelf-like.

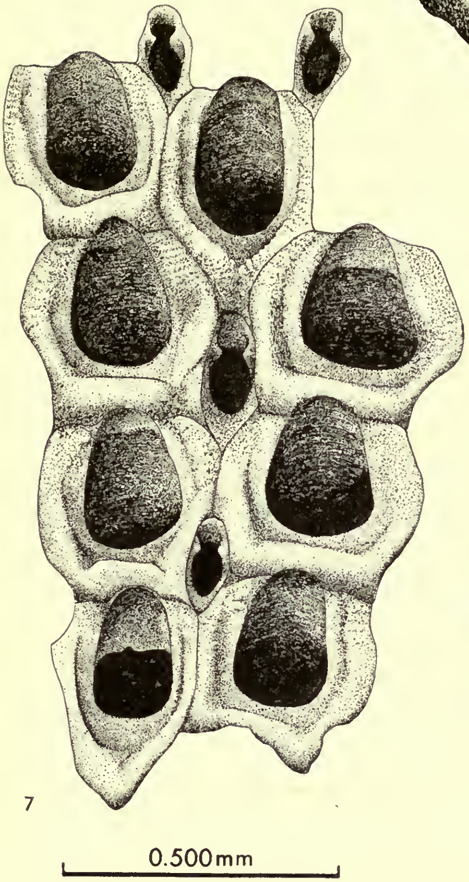
DESCRIPTION. *Zoarium* free in adult stages, discoidal, probably circular in outline, the upper surface moderately convex, the basal side slightly concave. Ancestrula encrusts *Nummulites* or small shell fragment which usually shows at centre of basal surface. Zooecia arranged in radial lines emanating from central ancestrula or from central fragment of an older zoarium from which regeneration has occurred. Vibracula occur in similar radial lines alternating with zooecia, one at every zooecial corner, except at points of intercalation of new zooecial rows. New zooecial rows originate from vibracular rows, the first zooecium of the new row lacking vibracula at its proximo-lateral corners, but having a single one proximally. Basal surface of zoarium with irregular, radial, finely perforated sectors, increasing in number peripherally by intercalation, separated by deep furrows.

Zooecia rhomboidal, slightly longer than wide, their mural rims confluent. Mural rim granular, broad and low laterally, but rising rapidly proximally to form a wide, thick, transverse wall separating cryptocyst of distal zooecium from opesia of proximal one. Cryptocyst a flat, imperforate, finely granular, very narrow shelf on proximal and lateral margins of opesia.

Opesia oval, more broadly rounded proximally than distally, without differentiated indentations.

Communication between zooecia by a single, large pore placed in middle of distal wall and a similar pore in each lateral wall.

Vibracula interzooecial, slightly shorter and much narrower than zooecia, rhombic, symmetrical, those of a series increasing in size distally. Vibracular opesia sym-



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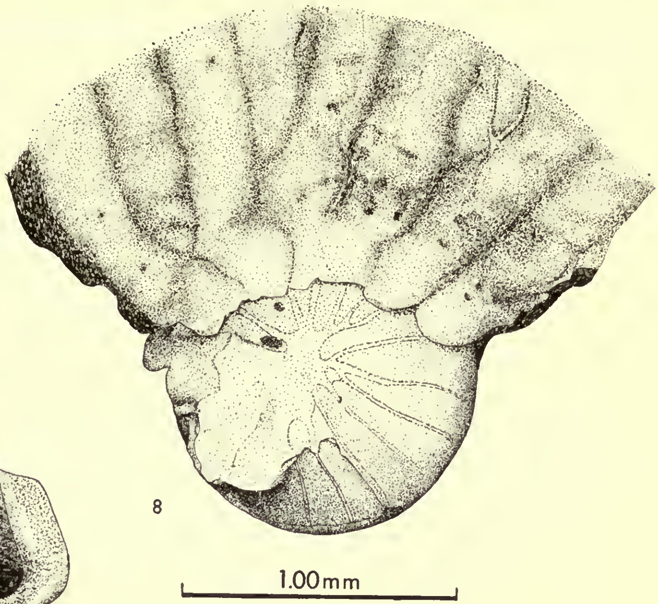

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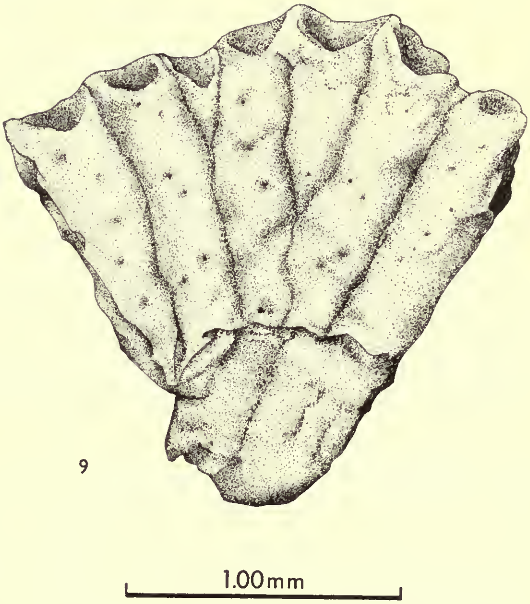

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FIGS. 7–9. Fig. 7. *Lunulites transiens* Gregory. D.48372. Eight zooecia and four vibracula. Zooecium at upper right is primoserial, budded from a vibraculum. Fig. 8. *Lunulites transiens* Gregory. D.48373. Basal aspect of a fragmentary zoarium emanating from a small Nummulitid test. Fig. 9. *Lunulites transiens* Gregory. D.48374. Basal aspect of a fragmentary zoarium regenerated from an older zoarial fragment.

metrical, oval, divided by a pair of stout condyles into a small distal portion and a much larger proximal one.

Ovicell lacking.

MEASUREMENTS :

Ordinary zooecia

Lz (5) 0·340 (0·0266) mm., 0·30–0·37 mm.
lz (5) 0·290 (0·0127) mm., 0·27–0·31 mm.
ho (5) 0·238 (0·0305) mm., 0·20–0·27 mm.
lo (5) 0·166 (0·0155) mm., 0·14–0·18 mm.

Primoserial zooecia

Lz (5) 0·398 (0·0239) mm., 0·36–0·42 mm.
lz (5) 0·260 (0·0076) mm., 0·26–0·27 mm.
ho (5) 0·231 (0·0326) mm., 0·20–0·24 mm.
lo (5) 0·137 (0·0086) mm., 0·13–0·14 mm.

Vibracula

Lv (5) 0·197 (0·0354) mm., 0·17–0·23 mm.
lv (5) 0·077 (0·0166) mm., 0·06–0·10 mm.

Vibracula proximal to primoserial zooecia

Lv (5) 0·327 (0·0245) mm., 0·30–0·36 mm.
lv (5) 0·162 (0·0270) mm., 0·14–0·20 mm.

REMARKS. Canu (1907*b* : 83), in re-describing and illustrating *L. urceolata* Lamarck, has given several criteria for the separation of the French Lutetian species from *L. transiens*. Of these, the shape of the zoarium and the development of the cryptocyst seem to be the most readily applicable.

The pattern of increase in number of zooecial rows exhibited by *L. transiens*, although distinctive, is by no means unique as Gregory (1893 : 233) implied. Among the American Tertiary species of *Lunulites*, *L. distans* Lonsdale and *L. fenestrata* (de Gregorio) show the same pattern. In *L. jacksonensis* (Canu & Bassler), *L. ligulata* (Canu & Bassler) and *L. tintinabula* (Canu & Bassler) increase is by bifurcation of zooecial rows ; in *L. bouei* Lea and *L. truncata* de Gregorio it is accomplished by bifurcation of vibracular rows with intercalation of zooecial rows between them. Among the European Tertiary species the *L. transiens* pattern seems to be much more widespread. Perhaps these patterns will make possible subgeneric partition of the very inclusive genus *Lunulites*.

DISTRIBUTION. Eocene (Auversian, Bartonian) ; England.

Family **ONYCHOCELLIDAE** Jullien

Genus ***ONYCHOCELLA*** Jullien

Onychocella subpyriformis (d'Archiac)

(Text-figs. 10, 11)

1846 *Eschara subpyriformis* d'Archiac : 195, pl. 5, figs. 21, 21*a*.
?1851 *Semieschara parisiensis* d'Orbigny : 366.
1869*a* *Membranipora angulosa* (Reuss) ; Reuss : 253, pl. 29, figs. 9–11.
1891 *Onychocella angulosa* (Reuss) Waters : 9.
1907*b* *Onychocella angulosa* (Reuss) ; Canu : 21, pl. 11, fig. 11.
1910 *Onychocella angulosa* (Reuss) ; Canu : 840, 844.
1916 *Onychocella angulosa* (Reuss) ; Faura y Sans & Canu : 298.
1925 *Onychocella angulosa* var. *parisiensis* (d'Orbigny) ; Canu : 46.
1926 *Onychocella angulosa* var. *parisiensis* (d'Orbigny) ; Canu : 748, pl. 27, fig. 7.
?1929 *Onychocella* n. sp., Burton : 328.
1929*a* *Onychocella angulosa* (Reuss) ; Canu & Bassler : 24.
1930 *Onychocella parisiensis* (d'Orbigny) ; Canu & Bassler : 22.
1933 *Onychocella parisiensis* (d'Orbigny) ; Dartevelle : 64, 106, 113.
1934 *Onychocella parisiensis* (d'Orbigny) ; Davis : 220.
1935 *Onychocella parisiensis* (d'Orbigny) ; Dartevelle : 112.
1936 *Onychocella parisiensis* (d'Orbigny) ; Dartevelle : 26.
1946 *Onychocella angulosa* var. *parisiensis* (d'Orbigny) ; Buge : 430.
1949 *Onychocella angulosa* (Reuss) ; Balavoine : 773.
1951 *Onychocella angulosa* (Reuss) ; Kyri : 71.
1956 *Onychocella parisiensis* (d'Orbigny) ; Balavoine : 321.
1957 *Onychocella angulosa* var. *parisiensis* (d'Orbigny) ; Balavoine : 191.
1960 *Onychocella parisiensis* (d'Orbigny) ; Balavoine : 246.
?1962 *Onychocella angulosa* (Reuss) ; Ghiurca, table 1.
?1963 *Onychocella angulosa* (Reuss) ; Malecki : 104, pl. 9, fig. 14.
1963 *Onychocella angulosa* (Reuss) ; Braga : 23, pl. 2, fig. 5.

FIGURED SPECIMENS. D.48431 (Text-fig. 10), D.48432 (Text-fig. 11).

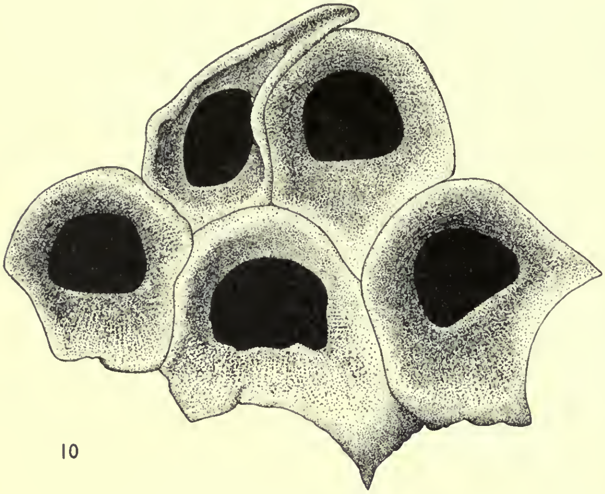
ADDITIONAL MATERIAL. Seventeen specimens, D.48433–D.48449.

DIAGNOSIS. *Onychocella* with zooecial opesia semi-circular, oval, or sub-pyriform and sub-terminal on cryptocyst, in some zooecia with distinct distal shelf ; opesiular indentations not differentiated ; avicularian opesia more broadly rounded distally than proximally.

DESCRIPTION. *Zoarium* encrusting, but probably rising in unilaminar, erect, tubular fronds, the zooecia arranged in irregular, alternating rows. Additional rows originate from an avicularium inserted between rows of zooecia.

Zooecia hexagonal, pentagonal, or rhomboidal, separated by a faint groove at the crest of the confluent mural rims. Zooecial length and width subequal, both extremely variable. Mural rim thin, sharp, and finely granular in most zooecia, but thickened and raised in some ; gymnocyst lacking. Cryptocyst extensive, markedly concave, present all round the opesia, widest proximally. Surface of cryptocyst imperforate, finely granular, merging with mural rim.

Opesia sub-terminal on the cryptocyst, extremely variable in size, semi-circular, oval, or sub-pyriform, the distal margin evenly rounded, the proximal margin straight, slightly convex, or slightly concave ; distinct distal shelf present in opesiae of zooecia with thickened mural rims. Opesiular indentations not differentiated from opesia.



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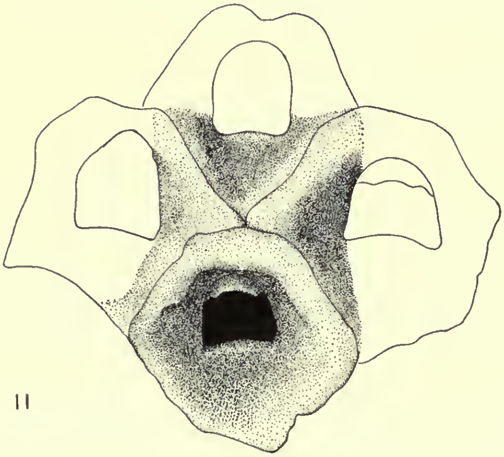

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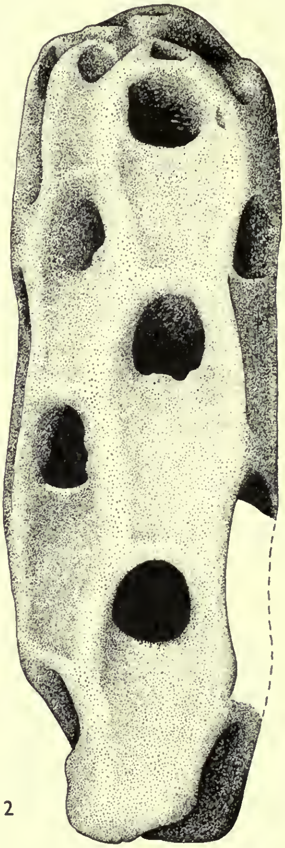

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Figs. 10–12. Fig. 10. *Onychocella subpyriformis* (d'Archiac). D.48431. Four zooecia and an onychocellarian avicularium. Fig. 11. *Onychocella subpyriformis* (d'Archiac). D.48432. Four zooecia partly shaded to show details of the raised and thickened mural rim and the distal opesial shelf of the zooecium at lower centre. Fig. 12. *Smittipora*? sp. D.48450. Fragment with worn and slightly broken zooecia.

Avicularia vicarious, longer but narrower than zooecia, with mural rim and cryptocyst identical with those of zooecia. Inwardly directed processes of mural rim separate elongate rostrum from short proximal part. Rostrum channelled, acutely pointed, directed sharply to either right or left, its axis diverging at angles of about 30° from main axis of avicularium. Avicularian opesia symmetrical, oval, more broadly rounded distally, sometimes pointed proximally, undivided by condyles or pivotal bar.

Ovicell lacking, but zooecia with nearly terminal opesiae may be fertile ones.

MEASUREMENTS :

Ordinary zooecia

Lz	(10) 0·362 (0·0557) mm., 0·31–0·49 mm.
lz	(10) 0·353 (0·0361) mm., 0·30–0·39 mm.
ho	(10) 0·153 (0·0153) mm., 0·13–0·18 mm.
lo	(10) 0·174 (0·0194) mm., 0·14–0·21 mm.

Zooecia with distal opesial shelf

ho	(5) 0·128 (0·0264) mm., 0·10–0·17 mm.
lo	(5) 0·133 (0·0076) mm., 0·13–0·14 mm.

Avicularia

Lav	(5) 0·506 (0·0305) mm., 0·46–0·55 mm.
lav	(5) 0·258 (0·0159) mm., 0·23–0·27 mm.
ho	(5) 0·171 (0·0121) mm., 0·15–0·18 mm.
lo	(5) 0·118 (0·0113) mm., 0·10–0·13 mm.

REMARKS. Canu (1910 : 844) recognized that d'Archiac's species is the same as the Eocene species identified by most authors with *O. angulosa* (Reuss), but, when he sorted the species out (1926 : 748), he used the unfortunate (and junior) name *Onychocella parisiensis* (d'Orbigny). The synonymy is further complicated by the existence of two Cretaceous species of *Onychocella*, *O. subpyriformis* (Hagenow) and *O. parisiensis* (d'Orbigny), whose names are homonyms of the Eocene species.

O. angulosa s.s., the Oligocene-Recent type species of *Onychocella*, is distinguished from *O. subpyriformis* by its sub-central opesia and its less angulated avicularian rostrum (see Reuss 1848 : pl. 11, fig. 10 ; Harmer 1926 : pl. 16, fig. 8).

DISTRIBUTION. Eocene (Lutetian, Auversian) ; France. Eocene (Auversian, Bartonian) ; Belgium, Spain. ?Eocene (Bartonian) ; England. Eocene (Ludian) ; Italy, Rumania, ?Poland.

Genus ***SMITTIPORA*** Jullien

Smittipora? sp.

(Text-fig. 12)

FIGURED SPECIMEN. D.48450 (Text-fig. 12).

Description. *Zoarium* erect, cylindrical, slender, composed of 6 longitudinal rows of zooecia alternating in position.

Zooecia separated by faint grooves at crest of confluent mural rims, rhomboidal to claviform ; length slightly less than twice width. Gymnocyst lacking. Mural rim worn, rather thick. Cryptocyst extends about two-thirds zooecial length from proximal margin ; surface slightly depressed, perceptibly concave, merging with mural rim peripherally, granular, imperforate.

Opesia terminal on cryptocyst, sub-circular, more broadly rounded proximally than distally, without differentiated indentations.

Heterozooecia, ovicells not present.

Measurements :

Lz (5) 0·446 (0·0496) mm., 0·38–0·50 mm.
lz (5) 0·253 (0·0155) mm., 0·23–0·27 mm.
ho (5) 0·135 (0·0153) mm., 0·11–0·14 mm.
lo (5) 0·125 (0·0177) mm., 0·10–0·14 mm.

Remarks. This species, represented solely by the fragment illustrated, resembles *Smittipora midwayanica* Canu & Bassler (1920 : 225, pl. 4, figs. 16–19) from the Palaeocene of Arkansas, U.S.A. It differs from the latter species in having fewer rows of larger zooecia with shorter opesiae. It also resembles *Glauconome prismatica* Hagenow and *G. canalifera* Hagenow, Cretaceous species often referred erroneously to *Vincularia* (see Berthelsen 1962 : 67–69). *Siphonella cylindrica* Hagenow is another Cretaceous form with similar zooecial and zoarial morphology but with a hollow zoarium (see Voigt 1951 : 61, 62). The generic assignment of these so-called vincularian forms can be resolved better by instituting a new genus for them than by distorting the Farciminariid genus *Vincularia* to accommodate them (see discussion of that genus below).

Family **MICROPORIDAE** Gray

Genus ***MICROPORINA*** Levinsen

1909 *Microporina* Levinsen : 162.

Type species (chosen by Bassler 1935). *Cellularia articulata* Fabricius 1824 : 27 (as *Salicornaria borealis* Busk 1855 : 254, pl. 1, figs. 1–3). Recent ; Greenland, 73° 20′ N., 57° 20′ W., 6–10 fms.

Diagnosis. Frontal wall membranous, without gymnocyst. Cryptocyst completely developed, shallow, flat, not greatly depressed in region of opesiules, finely and evenly perforate. Opesia approximately co-extensive with orifice, terminal, semi-circular to elliptical, with straight, slightly concave, or slightly convex proximal lip. Opesiules simple, small, circular or elliptical, inconspicuous, paired, one placed on each side of opesia and just proximal to it. Some of lateral cryptocystal pores probably serve as auxiliary opesiules in some species. Avicularia common or rare (or absent?), interzooecial, small, with pivotal bar and pointed rostrum, developed between zooecia of the same longitudinal row. Zooecia variable in size and shape, even in a single colony. Zoarium encrusting, erect-unilaminar or erect-jointed.

REMARKS. This genus differs from *Calpensia* in having avicularia, from *Micropora* in lacking ovicells, and from both in having simple, not tubular opesiules. Kluge (1962 : 322) has done much to clarify the characters of the genus and its type species.

Microporina magnipora (Canu)

(Text-figs. 13, 14)

1914*a* *Micropora magnipora* Canu : 299, pl. 4, figs. 1, 2.
?1963 *Steginoporella elegans* (Milne Edwards) ; Malecki : 111, pl. 11, fig. 6.

FIGURED SPECIMENS. D.48451 (Text-fig. 13), D.48452 (Text-fig. 14).

ADDITIONAL MATERIAL. Fifteen specimens, D. 48453–D.48467.

DIAGNOSIS. Unilaminar, encrusting to erect *Microporina* with large, rhomboidal zooecia ; opesiules not much larger than frontal pores ; avicularia lacking (?).

DESCRIPTION. *Zoarium* unilaminar, encrusting or forming erect, flat or hollow-tubular masses, composed of zooecia arranged in regular, occasionally bifurcating, longitudinal rows, those in adjacent rows alternating in position.

Zooecia separated by a very faint groove, rhomboidal, but becoming distorted or abortive in some parts of zoarium. Length almost twice width. Gymnocyst lacking. Mural rim finely granular, rounded, narrow distally, widening slightly proximally, raised round distal margin of opesia to form a half-collar. Interzooecial communication by a few large pores in lower half of distal and lateral walls.

Cryptocyst complete, extending from proximal margin more than three-quarters of the zooecial length. Surface nearly flat, depressed well below level of mural rim, deepest at centre, evenly perforated by large, quincuncially arranged pores, of which the lateral ones probably served as auxiliary opesiules. Opesiules simple pores, occasionally with slightly raised margins, one placed in each of the two disto-lateral corners of the cryptocyst, just proximal to opesia.

Opesia semi-circular, terminal, approximately co-extensive with orifice. Distal margin evenly rounded. Proximal margin nearly straight, but usually broken.

Avicularia and *ovicells* not present.

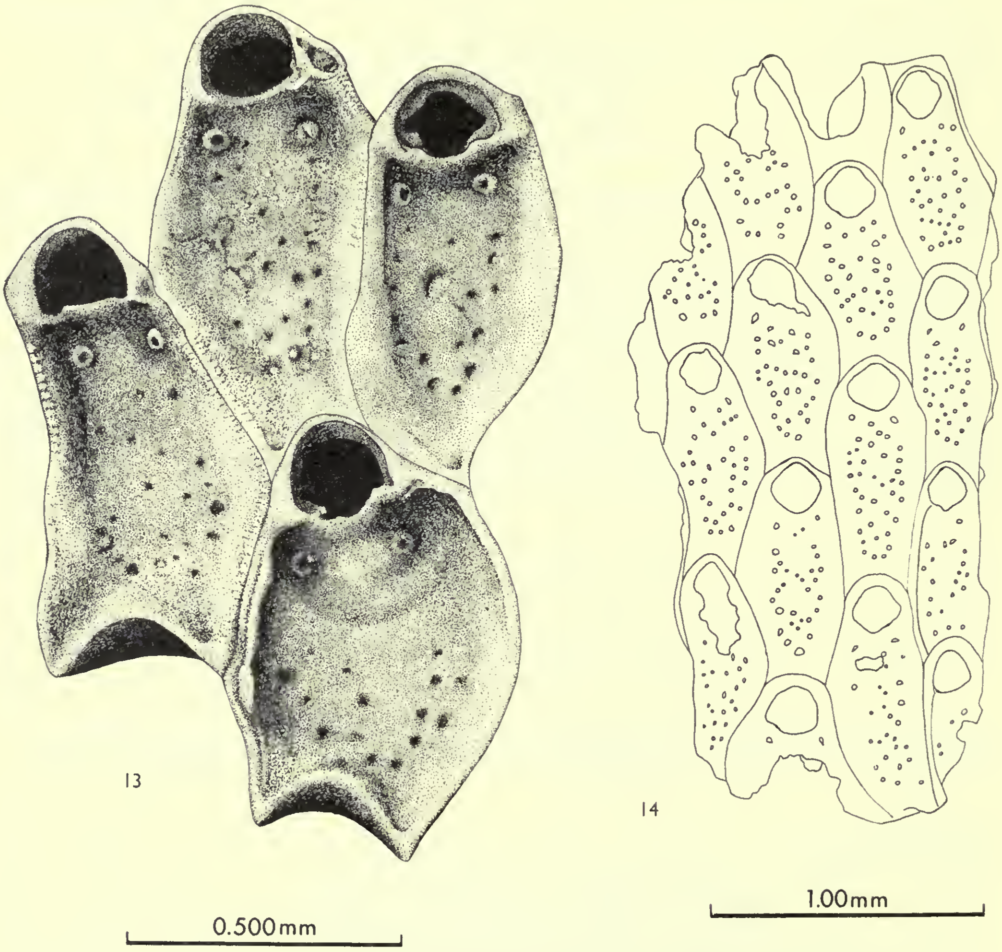
MEASUREMENTS :

Lz (10) 0·742 (0·0450) mm., 0·66–0·81 mm.
lz (10) 0·398 (0·0497) mm., 0·34–0·50 mm.
ho (6) 0·151 (0·0064) mm., 0·14–0·15 mm.
lo (10) 0·180 (0·0102) mm., 0·17–0·20 mm.

REMARKS. This species is very similar in both zooecial and zoarial characters to *Poropeltarion lebanonense* Cheetham (1963*b* : 50, pl. 1, figs. 5, 11) and *P. newelli*

Cheetham (1963*b* : 51, pl. 1, figs. 9, 10) from the Middle and Upper Eocene of Florida, U.S.A., but my suggestion (Cheetham 1963*b* : 50) that *M. magnipora* may belong to *Poropeltarion* has not been substantiated. The clearly differentiated opesiules of *M. magnipora* indicate that it should be assigned to *Microporina* despite the absence of avicularia. Dr. H. D. Thomas (personal communication, 1962) reports that a species of *Microporina* from the London Clay has avicularia only very occasionally. Whether *M. magnipora* proves to have avicularia or not, it forms a link with the slightly younger American *Poropeltarion*.

Distribution. Eocene (Lutetian) ; France. ?Eocene (Ludian) ; Poland.



Figs. 13–14. Fig. 13. *Microporina magnipora* (Canu). D.48451. Four zooecia from a slightly irregular part of a zoarium, probably near a point of branching. Fig. 14. *Microporina magnipora* (Canu). D.48452. Fragmentary zoarium showing more regularly arranged zooecia.

Genus ***SETOSELLA*** Hincks

1877 *Setosella* Hincks : 529.

TYPE SPECIES (by original designation). *Membranipora vulnerata* Busk 1860 : 124, pl. 25, fig. 3. Recent; British Isles.

DIAGNOSIS. Frontal wall membranous, with reduced gymnocyst laterally and proximally. Cryptocyst completely developed, imperforate except for a pair of lateral, longitudinal, slit-like opesiules near lateral margins. Opesia small, semicircular, terminal, co-extensive with orifice. Vibracula (missing in some species?) small, interzooecial, one at the distal end of each zooecium, the vibracular opesia reniform. Ovicell lacking, but fertile zooecia with swollen distal wall exhibiting a small depressed area and usually with a widened opesia.

REMARKS. Jullien (1882 : 524, pl. 17, fig. 66) was the first to describe and illustrate fertile zooecia in the type species of *Setosella*, but he interpreted them as having entotoichal (= " cassiform ") ovicells. This interpretation led Levinsen (1909 : 196) to establish a family, Setosellidae, to which later authors added *Entomaria* Duvergier (see discussion of the ovicell of that genus below) and other genera (see Bassler 1953 : 174). Material of *S. vulnerata* in the Department of Zoology, British Museum (Natural History), e.g. 99.7.1.1490, Busk Collection, shows the structure of the gonoecium clearly : the " ovicell " is simply a post-oral swelling in the distal wall not separated internally from the zooecium, and the " pore " is simply a frontal depression on the distal part of the gonoecium.

Absence of a distinct ovicell, as well as differences in zooecial structure, makes it necessary to remove *Setosella* from such genera as *Lagarozoum*, *Entomaria*, *Cratero-pora*, and *Aspidostoma*, for which the family name Aspidostomatidae Jullien is available (see Brown 1952 : 148–153). *Setosella* can be given temporary accommodation in the Microporidae.

Setosella fragilis Canu

(Text-figs. 15, 16)

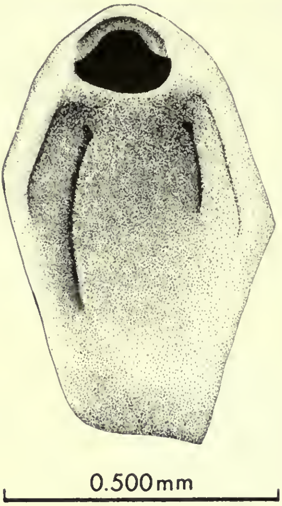
1907*b* *Setosella fragilis* Canu : 140, pl. 19, fig. 15.
1946 *Setosella fragilis* Canu; Buge : 433.

FIGURED SPECIMEN. D.48468 (Text-figs. 15, 16).

DIAGNOSIS. Erect, cylindrical *Setosella* arising from encrusting base ; zooecia without gymnocyst ; vibracula lacking ; gonoecia unknown.

DESCRIPTION. *Zoarium* erect, cylindrical, presumably arising from an encrusting base, the zooecia arranged in 8 longitudinal rows, those in adjacent rows alternating in position.

Zooecia regularly rhomboidal, rounded distally, straight sided proximally, separated by a faint groove at the crest of the confluent mural rims. Length about one and a half times width. Gymnocyst lacking. Mural rim smooth, probably abraded in the specimen studied, narrow all round the zooecium, not raised distally.



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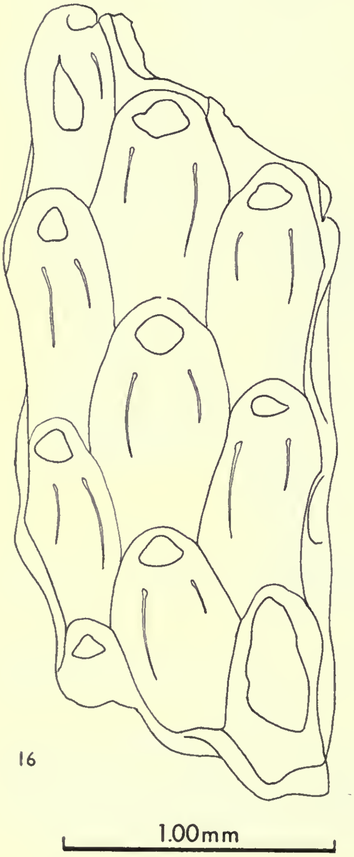

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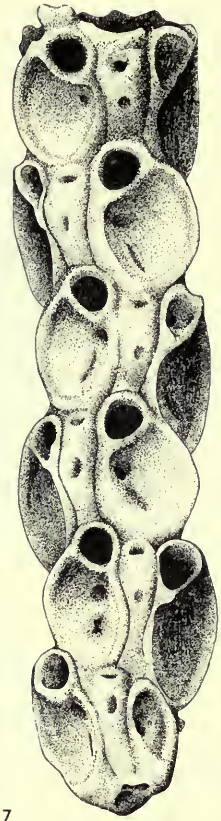

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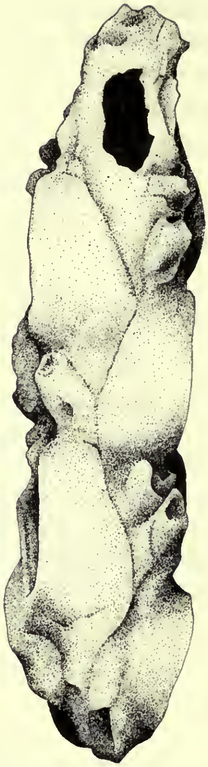

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Cryptocyst completely developed, extending from proximal margin more than three-quarters of the zooecial length. Surface somewhat undulating, convex and little depressed in proximal third, concave and moderately depressed in middle third, rising markedly in distal third; imperforate and smooth. Opesiules slit-like, unequal, one paralleling each lateral margin, removed slightly from mural rim. Longer opesiule, either right or left, markedly arcuate, extending from near proximal lip of opesia almost the whole length of the cryptocyst. Shorter opesiule less arcuate, extending from near proximal lip of opesia about half the length of the cryptocyst.

Opesia semi-elliptical, terminal, approximately co-extensive with orifice. Distal margin evenly rounded. Proximal margin much more broadly rounded.

Heterozooecia and *gonoecia* not observed.

MEASUREMENTS:

Lz	(7) 0·757 (0·0209) mm., 0·70–0·81 mm.
lz	(7) 0·486 (0·0340) mm., 0·44–0·54 mm.
ho	(7) 0·134 (0·0095) mm., 0·13–0·15 mm.
lo	(7) 0·184 (0·0197) mm., 0·15–0·20 mm.

REMARKS. My earlier suggestion (Cheetham 1963*b*: 50) that this species might belong to *Poropeltarion* has proved erroneous. The imperforate cryptocyst and slit-like opesiules exclude it from that genus. Although *S. fragilis* lacks gonoecia and vibracula, its original placement (Canu 1907*b*: 140) in *Setosella* seems to be correct. The species is represented in the Upper Bracklesham collection by the single fragment illustrated.

Canu's (1907*b*: pl. 19, fig. 15) restoration of the opesiules does not indicate their characteristically unequal lengths.

DISTRIBUTION. Eocene (Lutetian); France.

Family **PORICELLARIIDAE** Harmer

Genus ***PORICELLARIA*** d'Orbigny

1854 *Poricellaria* d'Orbigny: 1106.
?1869*b* *Diplodidymia* Reuss: 468.

TYPE SPECIES (by original designation). *Poricellaria alata* d'Orbigny 1854: 1106. Eocene (Lutetian); vicinity of Paris, France.

DIAGNOSIS. Frontal wall membranous, gymnocyst well developed. Cryptocyst completely developed, perforate or imperforate, with single or multiple, slit-like opesiule lying along one side only. Opesia small, terminal, semi-circular, oblique, approximately co-extensive with orifice. Avicularium adventitious, small, placed

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FIGS. 15–18. Figs. 15, 16. *Setosella fragilis* Canu. D.48468. Views of one zooecium and entire zoarial fragment. Fig. 17. *Poricellaria alata* d'Orbigny. D.48469. Frontal view of an internode fragment showing four rows of zooecia. Fig. 18. *Poricellaria alata* d'Orbigny. D.48470. View of reverse side of internode fragment with frontal surfaces hidden.

on proximal gymnocyst. Ovicell lacking. Zoarium erect, jointed, giving off basal rootlets. Internodes composed of 4 longitudinal rows of zooecia, one row on each face, but with orifices turned so as to open on the same face.

REMARKS. The Eocene species of *Poricellaria*, including *P. alata*, *P. limanowskii* (Canu) (1907*b* : 143, pl. 19, fig. 8) and *P. vernoni* Cheetham (1963*b* : 52, pl. 1, figs. 7, 8), differ from the Oligocene–Recent species, including *P. complicata* (Reuss) (see Canu 1914*b* : 467, pl. 14, figs. 11, 12) and *P. ratoniensis* (Waters) (see Harmer 1926 : 314, pl. 23, figs. 3–8), in having the frontal surfaces of all zooecia hidden when the zoarium is viewed from the reverse side (see *P. alata*, Text-fig. 18), in having the opesia less oblique to the zooecial axis, and in having the avicularium proportionately smaller. These differences suggest that *Diplodidymia*, of which *P. complicata* is the type species, should possibly be reinstated as a subgenus for the Neogene forms.

Poricellaria alata d'Orbigny

(Text-figs. 17, 18)

1854 *Poricellaria alata* d'Orbigny : 1106.
?1886 *Cellularia diplodidymioides* Meunier & Pergens : 3, pl. 2, fig. 3.
1891 *Micropora articulata* Waters : 14, pl. 2, figs. 5, 6.
1907*b* *Diplodidymia alata* (d'Orbigny) Canu : 143, pl. 19, fig. 7.
?1907*b* *Diplodidymia crassomuralis* Canu : 144, pl. 19, fig. 6.
?1907*b* *Diplodidymia negrisi* Canu : 144, pl. 19, figs. 9, 10.
1933 *Diplodidymia alata* (d'Orbigny) ; Dartevelle : 74.
1935 *Diplodidymia alata* (d'Orbigny) ; Dartevelle : 112, text-fig. 1.
1946 *Diplodidymia alata* (d'Orbigny) ; Buge : 431.
?1946 *Diplodidymia crassomuralis* Canu ; Buge : 432.
?1946 *Diplodidymia negrisi* Canu ; Buge : 432.
1957 *Poricellaria alata* d'Orbigny ; Balavoine : 191.
1960 *Poricellaria alata* d'Orbigny ; Balavoine : 246.
1962 *Poricellaria alata* d'Orbigny ; Davis : 194.

FIGURED SPECIMENS. D.48469 (Text-fig. 17), D.48470 (Text-fig. 18).

DIAGNOSIS. *Poricellaria* with frontal surfaces of all 4 zooecial rows visible in obverse aspect, reverse side showing basal surfaces of 2 rows ; opesial bisectrices of all rows make angles of 30°–45° with main axis ; proximal-gymnocystal avicularium small, placed obliquely ; opesiules single or double, distal one circular, proximal one slit-like.

DESCRIPTION. *Zoarium* erect, jointed. Internodes triangular in cross-section, with zooecia arranged in 4 longitudinal rows, all with frontal surface visible in obverse aspect, the zooecia of adjacent rows alternating in position. Proximal end of internode bluntly tapering, formed by 2 zooecia one of which is reduced and " membraniporoid ", the other normal but with a single, simple, proximal opening. Distal end not preserved.

Zooecia elongate club-shaped, asymmetrical, curved towards mid-line of obverse side. Zooecial length more than twice width. Gymnocyst about half zooecial length, smooth, convex, limited to proximal end of zooecium. Mural rim thin, sharp, smooth.

Cryptocyst completely developed, concave, deepest just proximal to opesia. Surface smooth, imperforate except for opesiule. Opesiule single or double, the distal one circular, the proximal one slit-like, placed on same side of cryptocyst, nearer zoarial mid-line (as viewed frontally).

Opesia semi-circular, oblique, its bisectrix making angles of 30°–45° with axis of internode. Proximal lip straight, as high as mural rim.

Avicularium adventitious, small, placed on proximal gymnocyst, the chamber oriented longitudinally and opening just below cryptocyst. Rostrum rounded, short, directed obliquely distally and outwards. Pivotal condyles or bar lacking. Proximal portion with a small pit or perforation.

Ovicell lacking.

MEASUREMENTS :

Lz (6) 0·453 (0·0276) mm., 0·43–0·51 mm.
lz (5) 0·185 (0·0167) mm., 0·16–0·20 mm.
ho (5) 0·068 (0·0086) mm., 0·06–0·08 mm.
lo (4) 0·086 (0·0000) mm., 0·09 mm.
Lav (4) 0·075 (0·0128) mm., 0·06–0·09 mm.

REMARKS. It is impossible to assess Dartevelle's interpretation (1935 : 112–114) of Meunier & Pergens's and Canu's species of *Poricellaria* as growth stages of *P. alata* until additional Lutetian and Montian material can be studied in detail. In the Recent *P. ratoniensis* the zooecia of the proximal internodes bear no resemblance to the normal, mature zooecia (see Harmer 1926, pl. 17, fig. 14), rather than being only slightly different as are *P. limanowskii*, *P. crassomuralis*, *P. negrisi*, *P. diplodidymioides* and *P. alata*. Preliminary study of specimens from the Sables de Fresville, Gourbesville (Manche), France (collected by Mr. Dennis Curry), suggests that *P. limanowskii*, at least, is a separate species from *P. alata*.

Waters's (1891 : 15) description of the avicularia of *P. alata* as vibracula was apparently based on his interpretation of the avicularian proximal pits as vibracular pores. Similar pits occur on the avicularia of *P. ratoniensis* (see Harmer 1926, pl. 23, figs. 6–8).

DISTRIBUTION. ?Palaeocene (Montian) ; Belgium. Eocene (Lutetian) ; France. Eocene (Auversian) ; England. Eocene (Ludian) ; Italy.

Family **STEGANOPORELLIDAE** Hincks

Genus ***LABIOPORELLA*** Harmer

Labioporella*? *dartevellei[7] sp. nov.

(Text-figs. 19–22)

1851 " *Eschara fragilis* (Michelin), *non* Defrance " ; d'Orbigny : 344.
1907*b* " *Smittipora fragilis* (d'Orbigny) " ; Canu : 80, pl. 11, figs. 5–7.
?1933 *Steganoporella fragilis* Dartevelle : 74, pl. 2, fig. 2.

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[7] After the late Edmond Dartevelle.

1946 "*Smittipora fragilis* (d'Orbigny)"; Buge: 431.
1949 "*Smittipora fragilis* (d'Orbigny)"; Balavoine: 773.
1956 "*Smittipora fragilis* (d'Orbigny)"; Balavoine: 320, 324.
1957 "*Smittipora fragilis* (d'Orbigny)"; Balavoine: 191.
1960 "*Smittipora fragilis* (d'Orbigny)"; Balavoine: 246.
?1962 "*Smittipora fragilis* (d'Orbigny)"; Gorodiski & Balavoine: 5.

HOLOTYPE. D.48471 (Text-figs. 19–21).

PARATYPES. D.48472 (Text-fig. 22), D.48473–75 (3 specimens), L.S.U. 8033.

DIAGNOSIS. *Labioporella* (?) with rudimentary zooecial dimorphism, the avicularian (?) zooecia differing only in size from the normal ones; polypide tube short, wide, slightly eccentric; mural rim smooth; zoarium eschariform with edges bevelled owing to compression of zooecia of marginal rows.

DESCRIPTION. *Zoarium* erect, bilaminar, compressed, with zooecia arranged in 2–7 longitudinal rows on each side, those in adjacent rows alternating in position. Number of zooecial rows increases distally by bifurcation. Lateral margins of zoarium with bevelled appearance produced by compression of zooecia of marginal rows.

Zooecia rhomboidal to sub-rectangular, not markedly dimorphic, with evenly rounded distal borders, separated by a faint groove. Length about twice width. Mural rim smooth, thin and rather sharp distally, thicker and rounded proximally. Gymnocyst lacking.

Cryptocyst broad, fully developed, flat and shallow proximally, concave and steeply descending distally, evenly perforated with numerous, small, quincuncially arranged pores. Distal portion reflected upwards, except at lateral extremities, to form short, wide, slightly eccentric polypide tube with fully developed basal portion.

Opesia semi-circular, sub-terminal, with very narrow distal shelf. Opesiular indentations shallow, not well defined, unequal.

Avicularian (?) *zooecia* slightly larger than ordinary ones, but not different in form.

Ovicells lacking.

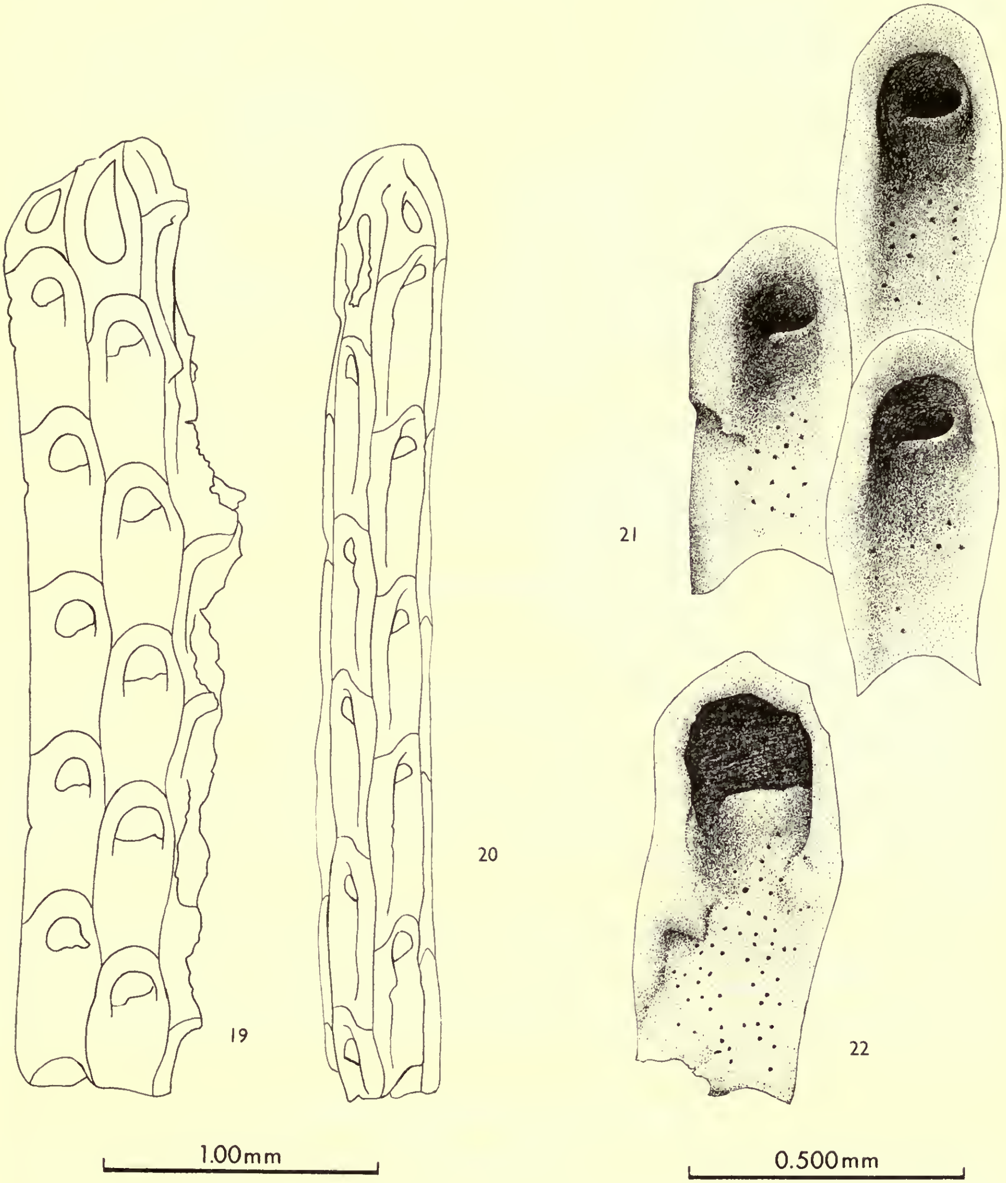
MEASUREMENTS:

Ordinary zooecia

Lz (9) 0·577 (0·0317) mm., 0·53–0·65 mm.
lz (9) 0·264 (0·0304) mm., 0·20–0·30 mm.
ho (6) 0·121 (0·0114) mm., 0·10–0·13 mm.
lo (6) 0·131 (0·0279) mm., 0·10–0·17 mm.

Avicularian (?) zooecia

Lz (2) 0·761 (0·0605) mm., 0·72–0·80 mm.
lz (2) 0·325 (0·0242) mm., 0·31–0·34 mm.
ho (1) 0·19 mm.
lo (1) 0·23 mm.



FIGS. 19–22. Figs. 19–21. *Labioporella*? *dartevellei* sp. nov. D.48471. Holotype. Front and edge views of fragmentary zoarium and details of three ordinary zooecia. Edge view shows bevelling produced by compression of marginal zooecia. Fig. 22. *Labioporella*? *dartevellei* sp. nov. D.48472. Paratype. Avicularian (?) zooecium.

REMARKS. This widespread Eocene species has been a nomenclatorial puzzle for at least a hundred years since d'Orbigny mis-identified it with Michelin's (1845: 176) material which he considered to have been in turn mis-identified with Defrance's (1828: 428) species. Whether Michelin and Defrance had the same species or not, both of them had a different one from the present species: their illustrations show cylindrical, tubular zoaria with zooecia having sub-central opesiae. Canu (1907*b*: 80, pl. 11, figs. 5–7) re-described and, for the first time, illustrated d'Orbigny's material but, unfortunately, did not re-name it. Dartevelle (1933: 74, pl. 2, fig. 2), who possibly had the same species, coined a new, but unfortunately homonymous, name for it.

French Lutetian specimens (Canu, 1907*b*: pl. 11, figs. 5–7) have many of the zooecia closed, especially along the zoarial margins, or with degenerated cryptocysts. Zooecia in the latter condition may represent fertile zooecia of the type noted by Cook (1964: 51, 52) in various species of *Steganoporella*; cryptocystal degeneration was not, however, noted by her in *Labioporella*.

This species does not fit well in either *Labioporella* or *Steganoporella* but seems closer to the former because of the asymmetrical polypide tube and the lack of a wide distal shelf in the avicularian (?) zooecia.

DISTRIBUTION. Eocene (Lutetian); France, ?Senegal. ?Eocene (Auversian); Belgium.

Genus *GAUDRYANELLA* Canu

1900 *Gaudryanella* Canu: 380 (nomen nudum).
1907*b* *Gaudryanella* Canu: 141.

TYPE SPECIES (by monotypy). *Gaudryanella variabilis* Canu 1907*b*: 142, pl. 19, figs. 17–20. Eocene (Lutetian); vicinity of Paris, France.

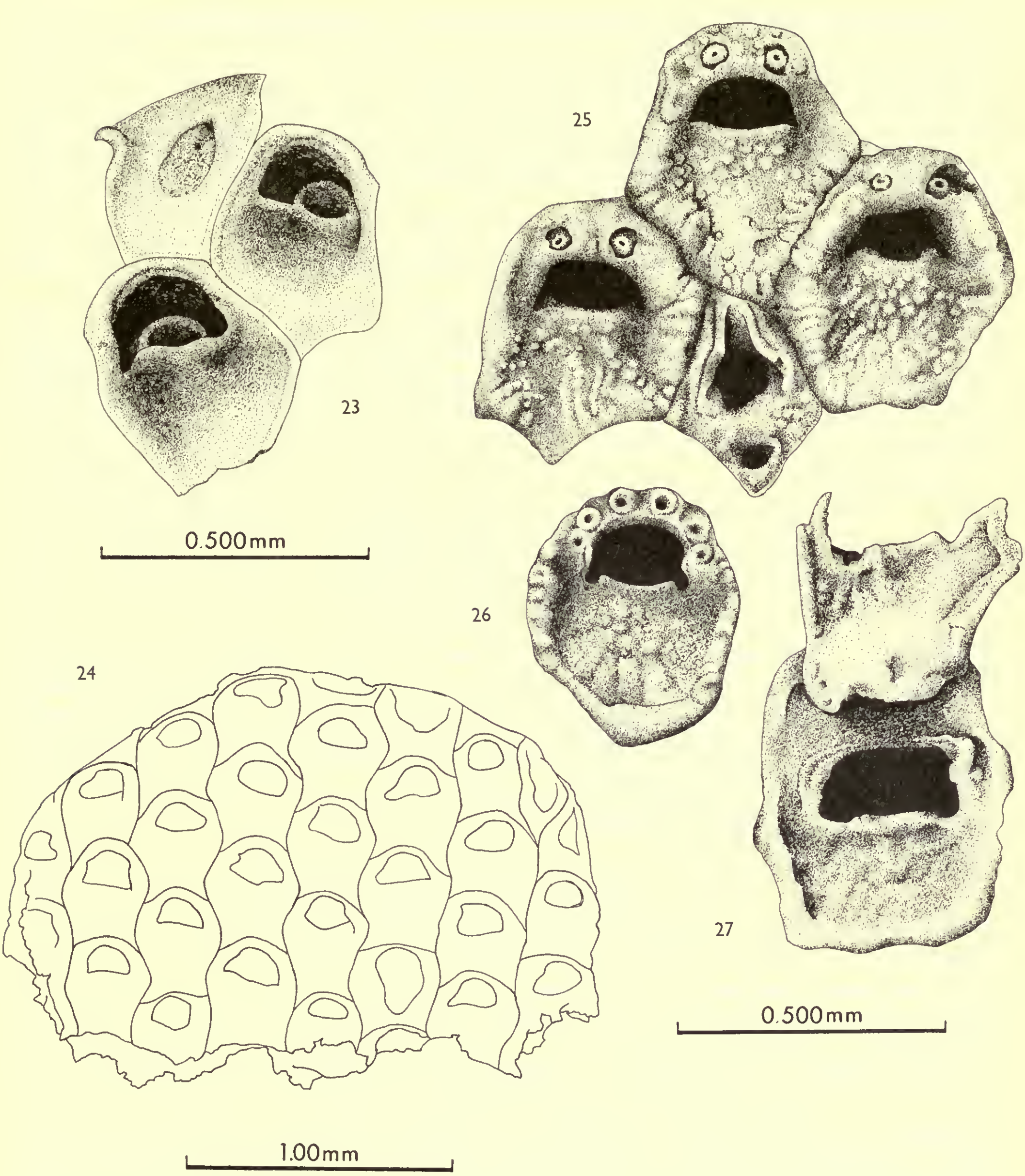
DIAGNOSIS. Frontal wall membranous, gymnocyst lacking. Cryptocyst imperforate, fully developed, markedly concave, descending steeply to basal wall distally so as to form a small, eccentric polypide tube. Opesia large, terminal, with irregular, unequal opesiular indentations. Zooecial dimorphism not apparent. Ovicell lacking.

REMARKS. The "large, ovarian zooecia", mentioned by Canu (1907*b*: 141) in the original diagnosis, may have been formed through wear or degeneration of the cryptocyst. The absence of cryptocystal pores and zooecial dimorphism in this genus distinguishes it from *Steganoporella* and *Labioporella*; the lack of a gymnocyst distinguishes it from *Siphonoporella*.

Gaudryanella variabilis Canu

(Text-figs. 23, 24)

1907*b* *Gaudryanella variabilis* Canu: 142, pl. 19, figs. 17–20.
1925 *Gaudryanella variabilis* Canu; Canu: 47.
1946 *Steganoporella variabilis* (Canu) Buge: 432.
1956 *Gaudryanella variabilis* Canu; Balavoine: 320, 324.
1957 *Steganoporella variabilis* (Canu); Balavoine: 191.
1960 *Gaudryanella variabilis* Canu; Balavoine: 246.



Figs. 23–27. Fig. 23. *Gaudryanella variabilis* Canu. D.48476. Two complete zooecia and a partially developed or degenerated one. Fig. 24. *Gaudryanella variabilis* Canu. D.48477. Fragmentary zoarium showing arrangement of zooecia. Fig. 25. *Entomaria dutempleana* (d'Orbigny). D.48482. Three mature zooecia and an avicularium. Fig. 26. *Entomaria dutempleana* (d'Orbigny). D.48483. A young zooecium with the spine bases not yet overgrown by conuli. Fig. 27. *Entomaria dutempleana* (d'Orbigny). D.48484. Ovicelled zooecium and part of the distal zooecium.

FIGURED SPECIMENS. D.48476 (Text-fig. 23), D.48477 (Text-fig. 24).

ADDITIONAL MATERIAL. Four specimens, D.48478–D.48481.

DIAGNOSIS. As for the genus (the only species).

DESCRIPTION. *Zoarium* uni- or bilaminar, erect, composed of wide fronds with zooecia arranged in 8 or more longitudinal rows, those in adjacent rows alternating in position.

Zooecia rhomboidal, rounded distally, straight proximally, separated by a very faint groove. Length and width subequal. Gymnocyst lacking. Mural rim thin, sharp, smooth, not distinctly raised.

Cryptocyst concave, deeply depressed at its distal end where it extends to basal wall to form a small, short, eccentric polypide tube. Surface smooth, imperforate.

Opesia large, asymmetrical, semi-circular, terminal. Opesiular indentations broad, shallow, unequal.

Heterozooecia and *ovicells* lacking.

MEASUREMENTS :

Lz	(10)	0·363	(0·0345) mm.,	0·32–0·40 mm.
lz	(10)	0·354	(0·0474) mm.,	0·27–0·44 mm.
ho	(10)	0·131	(0·0128) mm.,	0·11–0·14 mm.
lo	(10)	0·189	(0·0272) mm.,	0·15–0·21 mm.

REMARKS. The only suggestion of departure from the morphology of the ordinary zooecia in the Upper Bracklesham material is in a partially developed or degenerate zooecium (Text-fig. 23) in one fragment and several slightly reduced primoserial zooecia in another. None of these seems to fit the description given by Canu (1907*b* : 141) of " ovarian " zooecia.

DISTRIBUTION. Eocene (Lutetian) ; France.

Family **ASPIDOSTOMATIDAE** Jullien

Genus ***ENTOMARIA*** Duvergier

1921 *Entomaria* Duvergier : 150 (introduced in faunal list).
1927 " *Entomaria* Canu (*in* Duvergier) " ; Canu & Lecointre : 45.

TYPE SPECIES (by monotypy). *Rhagasostoma spiniferum* Canu 1914*b* : 469, pl. 15, fig. 7. Oligocene (Stampian) ; Gaas (Gironde), France.

DIAGNOSIS. Frontal wall membranous, gymnocyst narrow but encircling zooecium. Cryptocyst extensive, imperforate, merging with mural rim. Distal margin of mural rim with spine bases, often overgrown by conule-like extensions of distal gymnocyst. Opesia with lateral opesiular indentations and proximal cryptocyst-flange (= false polypide tube). Avicularia interzooecial, with opesiulated cryptocyst. Ovicell entozooecial.

REMARKS. This genus, often erroneously attributed to Canu (see Canu & Lecointre 1927 : 45), has been considered congeneric with *Lagarozoum* (see Bassler 1953 : 174), from which it differs in lacking distinct cryptocyst ridges and in having oral spines, though these are often overgrown by projections of the distal gymnocyst forming structures similar to the conuli of *Lagarozoum* (see Harmer 1926 : 325, pl. 22, fig. 6). The ovicell of *Entomaria*, a typical entozooecial chamber opening above the opesia and extending distally under the gymnocyst and proximal part of the cryptocyst of the next zooecium, has been misinterpreted as entotoichal (see Canu & Lecointre 1927 : 45).

Entomaria dutempleana (d'Orbigny)

(Text-figs. 25–27)

1851 *Semieschara dutempleana* d'Orbigny : 366.
1900 *Rhagasostoma dutempleanum* (d'Orbigny) Canu : 428, pl. 7, figs. 22, 23.
1907*b* *Rhagasostoma dutempleanum* (d'Orbigny) ; Canu : 138, pl. 5, fig. 12.
1915 *Rhagasostoma dutempleanum* (d'Orbigny) ; Canu : 297.
1925 *Entomaria dutempleana* (d'Orbigny) Canu : 47.
1927 *Entomaria dutempleana* (d'Orbigny) ; Canu & Lecointre : 45.
1935 *Entomaria dutempleana* (d'Orbigny) ; Dartevelle : 115.
1937 *Entomaria dutempleana* (d'Orbigny) ; Dartevelle : 110.
1946 *Entomaria dutempleana* (d'Orbigny) ; Buge : 433.
1957 *Entomaria dutempleana* (d'Orbigny) ; Balavoine : 191.
1960 *Entomaria dutempleana* (d'Orbigny) ; Balavoine : 246.

FIGURED SPECIMENS. D.48482 (Text-fig. 25), D.48483 (Text-fig. 26), D.48484 (Text-fig. 27).

ADDITIONAL MATERIAL. Forty specimens, D.48485–D.48524.

DIAGNOSIS. *Entomaria* with small zooecia and narrow gymnocyst ; ovicell small, without large lateral slits ; avicularia initiate new zooecial rows.

DESCRIPTION. *Zoarium* encrusting or erect, uni- or bilaminar, forming irregular, convoluted, hollow, tubular masses, the zooecia arranged more or less in longitudinal rows, those in adjacent rows alternating in position.

Zooecia ideally rhomboidal, straight sided, but often distorted or abortive, separated by distinct, sometimes deep furrows. Length and width subequal. Gymnocyst very narrow, but present entirely round zooecium. Mural rim wide, rounded, irregularly crenulated or beaded ; distal margin with 4–6 large, hollow spine bases, the more distal ones larger than the others ; distal gymnocyst grows over all but two of the spines to form a series of irregular hummocks or conuli. Zooecia communicate by simple pores placed near base of distal and lateral walls.

Cryptocyst extensive, covering nearly three-quarters of zooecial length. Surface nearly flat, highest near centre, deepest along lateral margins, imperforate, coarsely tuberculate, not distinctly marked off from mural rim. Distal part, along proximal lip of opesia, slightly raised to form a very narrow flange or false polypide tube.

Opesia semi-elliptical, much wider than high ; distal margin evenly and broadly rounded, provided with a very narrow distal shelf ; proximal margin scalloped, the broad cryptocystal flange limited on each side by a small, rounded opesiular indentation.

Avicularia interzooecial, initiating zooecial rows. Mural rim like that of zooecia but raised and pointed distally. Cryptocyst like that of zooecia but with one or two opesiules near proximal end. Opesia distal, oval. Spines and conuli absent.

Ovicell entozooecial, globular, opening over the opesia, the surface a tuberculate, imperforate awning projecting from the gymnocyst of the distal zooecium and discernible as a swelling under the proximal part of its gymnocyst. Ovicelled zooecia larger than ordinary ones, with larger opesia and without spines or conuli.

MEASUREMENTS :

Ordinary zooecia

Lz	(10) 0·494 (0·0623) mm., 0·41–0·62 mm.
lz	(10) 0·423 (0·0417) mm., 0·37–0·51 mm.
ho	(10) 0·122 (0·0274) mm., 0·09–0·16 mm.
lo	(10) 0·208 (0·0202) mm., 0·18–0·25 mm.

Ovicelled zooecia

Lz	(3) 0·596 (0·0623) mm., 0·53–0·65 mm.
lz	(3) 0·445 (0·0534) mm., 0·40–0·50 mm.
ho	(3) 0·140 (0·0049) mm., 0·14–0·15 mm.
lo	(3) 0·242 (0·0178) mm., 0·22–0·26 mm.

Avicularia

Lav	(7) 0·355 (0·0761) mm., 0·27–0·48 mm.
lav	(7) 0·227 (0·0430) mm., 0·17–0·29 mm.

REMARKS. Canu's description of the ovicell of this species as entotoichal (1925 : 47) cannot be verified in the present material. Though the opening of the ovicell is distal to the opesia, it is not far removed, and the ovicell chamber is immersed in the distal zooecium and covered by its gymnocyst and the proximal part of its cryptocyst.

DISTRIBUTION. Eocene (Lutetian) ; France, Belgium.

Family **FARCIMINARIIDAE** Busk

Genus ***NELLIA*** Busk

Nellia tenella (Lamarck)

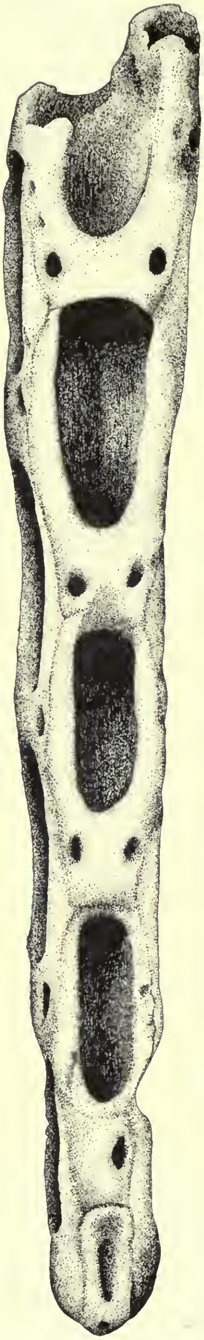
(Text-fig. 28)

1816 *Cellaria tenella* Lamarck : 135.
1851 *Cellaria tenella* Lamarck ; d'Orbigny : 28.
1851 *Cellaria quadrilatera* d'Orbigny : 29.
1852*a* *Salicornaria dichotoma* Busk : 367 ; *non* Schweigger, 1819.
1852*b* *Nellia oculata* Busk : 18, pl. 64, fig. 6 ; pl. 65, fig. 4.
1873 *Nellia oculata* Busk ; Smitt : 3, pl. 1, figs. 53, 54.
1880 *Nellia oculata* Busk ; MacGillivray : 51, pl. 49, figs. 5, 5*a*, *b*.
1881 *Nellia oculata* Busk ; Haswell : 36.
1883 *Membranipora oculata* (Busk) Waters : 434.

1887 *Farcimia oculata* (Busk) Waters : 92.
1887 *Nellia oculata* Busk ; Hincks : 121.
1895 *Farcimia oculata* (Busk) ; MacGillivray : 50, pl. 6, figs. 6, 7.
1905 *Nellia oculata* Busk ; Thornely : 110.
1905 *Farcimia quadrilatera* (d'Orbigny) Waters : 3.
1907 *Nellia oculata* Busk ; Thornely : 185.
1907*b* *Farcimia tenella* (Lamarck) Canu : 76, pl. 10, figs. 36, 37.
1907*b* *Farcimia bituberculata* Canu : 73, pl. 10, figs. 24–29.
1909 *Farcimia oculata* (Busk) ; Waters : 167.
1909 *Nellia tenella* (Lamarck) ; Levinsen : 120, pl. 1, figs. 13 *a–e*.
1912 *Farcimia oculata* (Busk) ; Canu : 191, pl. 10, figs. 16, 19.
1913 *Farcimia oculata* (Busk) ; Waters : 489, pl. 67, figs. 8, 9.
1914 *Nellia oculata* Busk ; Osburn : 191.
1916 *Farcimia bituberculata* Canu ; Faura y Sans & Canu : 298.
1920 *Nellia bifaciata* Canu & Bassler : 197, pl. 32, figs. 15–19.
1920 *Nellia oculata* Busk ; Marcus : 5.
1921 *Farcimia tenella* (Lamarck) ; Duvergier : 8.
1921 *Farcimia oculata* (Busk) ; Robertson : 45.
1921 *Nellia oculata* Busk ; Marcus : 3.
1922 *Nellia oculata* Busk ; Marcus : 423.
1923 *Nellia oculata* Busk ; Canu & Bassler : 55, pl. 2, figs. 5–7.
1926 *Nellia oculata* Busk ; Harmer : 240, pl. 14, figs. 18–20.
1927 *Nellia oculata* Busk ; Osburn : 125.
1928 *Nellia oculata* Busk ; Canu & Bassler : 26.
1929*b* *Nellia oculata* Busk ; Canu & Bassler : 185, pl. 5, figs. 12, 13.
1932 *Nellia oculata* Busk ; Hastings : 410.
1934 *Nellia tenella* (Lamarck) ; Davis : 220.
1935 *Nellia oculata* Busk ; Dartevelle : 115.
1935 *Nellia bituberculata* (Canu) Dartevelle : 115.
1940 *Nellia oculata* Busk ; Osburn : 400.
1941 *Nellia oculata* Busk ; McGuirt : 66, pl. 2, fig. 5.
1941 *Nellia oculata* Busk ; Silén : 49.
1944 *Nellia ocullata* [sic] Busk ; Pokorny : 1–14.
1946 *Farcimia tenella* (Lamarck) ; Buge : 433.
1946 *Farcimia bituberculata* Canu ; Buge : 433.
1947 *Nellia oculata* Busk ; Osburn : 25.
1949 *Farcimia bituberculata* Canu ; Balavoine : 773.
1949 *Nellia oculata* Busk ; Vigneaux : 32, pl. 1, figs. 10–12.
1950 *Nellia oculata* Busk ; Osburn : 119, pl. 13, fig. 4.
1956 *Nellia tenella* (Lamarck) ; Balavoine : 321.
1957 *Nellia bituberculata* (Canu) ; Balavoine : 191.
1957 *Nellia tenella* (Lamarck) ; Cheetham : 93.
1959 *Nellia oculata* Busk ; Lagaaij : 482, text-fig. 1.
1960 *Nellia tenella* (Lamarck) ; Balavoine : 246.
1962 *Nellia tenella* (Lamarck) ; Cheetham : 326, pl. 1, figs. 4, 5.
?1962 *Nellia tenella* (Lamarck) ; Gorodiski & Balavoine : 6.
?1962 *Farcimia bituberculata* Canu ; Gorodiski & Balavoine : 6.
1962 *Nellia oculata* Busk ; Ghiurca, table 1.
1963 *Nellia tenella* (Lamarck) ; Braga : 27.
1963*b* *Nellia tenella* (Lamarck) ; Cheetham : 59, pl. 1, fig. 14.

FIGURED SPECIMEN. D.48525 (Text-fig. 28).

ADDITIONAL MATERIAL. Five specimens, D.48526–D.48530.



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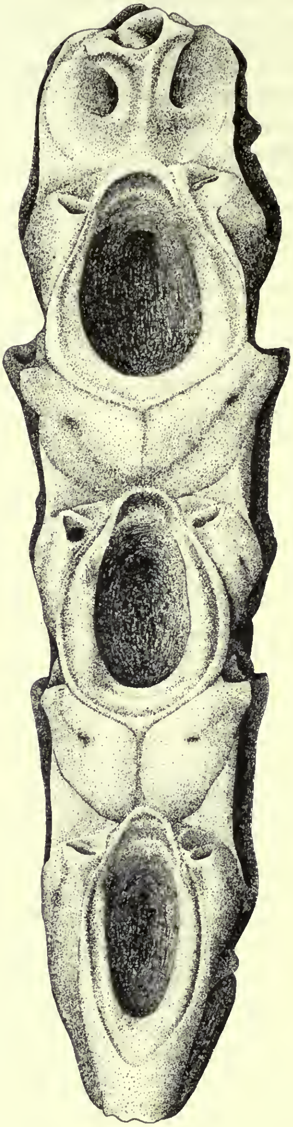

29

DIAGNOSIS. *Nellia* with relatively narrow zooecia of same width on all 4 faces of zoarium; avicularia paired, placed in proximo-lateral corners of gymnocyst, small, sometimes vestigial; proximal end of internode with 1 large and 2 smaller pores; distal end with 2 groups of such pores.

DESCRIPTION. *Zoarium* erect, delicate, articulated, dichotomously branching at nodes. Internodes long, slender, square in cross-section, the zooecia arranged in 4 longitudinal rows, those in adjacent rows alternating in position. Zooecia on all 4 faces subequal. Tips of articulating ends not preserved, but proximal portion consists of 2 normal and 2 greatly reduced zooecia.

Zooecia elongate, club-shaped, separated by distinct grooves. Length more than twice width. Gymnocyst smooth, convex, extending about a third of the zooecial length from the proximal margin. Mural rim smooth, sharp, slightly raised. Cryptocyst a narrow crescent on proximal margin of opesia; surface smooth, slightly concave, imperforate.

Avicularia adventitious, small, paired except on zooecia just distal to reduced zooecia at proximal end of internode, placed in proximo-lateral corners of gymnocyst, the rostrum directed distally and slightly outwards. Pivotal structures lacking in material at hand. Proximal part of avicularian chamber sometimes with a small pore.

Ovicell entozooecial, discernible as a slight swelling under gymnocyst of distal zooecium. Frontal depression lacking in material at hand. Opesia of ovicelled zooecium slightly enlarged.

MEASUREMENTS:

Ordinary zooecia

Lz (8) 0·525 (0·0214) mm., 0·50–0·56 mm.
lz (8) 0·205 (0·0216) mm., 0·17–0·24 mm.
ho (8) 0·358 (0·0367) mm., 0·32–0·41 mm.
lo (8) 0·119 (0·0140) mm., 0·10–0·14 mm.

Ovicelled zooecia

Lz (1) 0·57 mm.
lz (1) 0·26 mm.
ho (1) 0·42 mm.
lo (1) 0·18 mm.

Avicularia

Lav (10) 0·067 (0·0150) mm., 0·04–0·09 mm.

REMARKS. Although it is true, as Harmer (1926 : 242) has remarked, that the description given by Lamarck (1816 : 135) for *Cellaria tenella* is insufficient to separate it from other jointed species, the probability that Lamarck had this ubiquitous

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FIGS. 28–29. Fig. 28. *Nellia tenella* (Lamarck). D.48525. One face of broken internode showing four complete zooecia and a broken one. Proximal zooecium is reduced; distal complete zooecium is ovicelled. Fig. 29. *Nellia ventricosa* (Canu). D.48532. One face of broken internode showing three zooecia and a small portion of a fourth, distal one.

warm-water Cheilostome in his collection is very great. Moreover, even if Harmer was correct in discarding *C. tenella* from its synonymy, the next oldest available name is *C. quadrilatera* d'Orbigny, not *Nellia oculata* Busk.

Farcimia bituberculata Canu appears, from Canu's figures (1907*b*, pl. 10, figs. 24–29), to be the same as Harmer's (1926 : 242) " typical form " of *N. tenella* with vestigial avicularia.

The type specimens of *N. bifaciata* Canu & Bassler, U.S. National Museum Cat. Nos. 63954, 63955, have zooecia of different widths on different fragments, not on different faces of the same fragment, and are thus conspecific with *N. tenella.*

The Upper Bracklesham specimens differ from Recent *N. tenella* in having the functional avicularia without pivotal bar and the ovicell without the frontal depression (see Harmer 1926, pl. 14, figs. 19, 20 ; Osburn 1950, pl. 13, fig. 4). American Eocene specimens have the depression on the ovicell and some of the avicularia vestigial (see Cheetham 1962, pl. 1, figs. 4, 5).

DISTRIBUTION. Eocene (Lutetian) ; France, Spain, ?Senegal. Eocene–Oligocene (Claibornian, Jacksonian, Vicksburgian) ; Gulf Coast of U.S.A. Miocene ; Egypt, Jamaica, Australia. Recent ; tropical and warm-temperate zones of all oceans.

Nellia ventricosa (Canu)

(Text-fig. 29)

1914*a* *Quadricellaria ventricosa* Canu : 298, pl. 4, figs. 6, 7.
?1962 *Nellia ventricosa* (Canu) Gorodiski & Balavoine : 6.

FIGURED SPECIMEN. D.48532 (Text-fig. 29).

DIAGNOSIS. *Nellia* with short, stubby internodes, the proximal ends of which are formed by 2 opposing zooecia, each with a single, terminal opening ; gymnocyst and opesia of about equal length ; cryptocyst well developed ; avicularia large, paired, with chambers meeting on proximal gymnocyst and opening over opesiae of adjoining rows.

DESCRIPTION. *Zoarium* erect, jointed, probably branching at nodes. Internodes short, square in cross-section, with zooecia arranged in longitudinal rows, one row of 3–4 zooecia on each face, the zooecia of adjacent rows alternating in position. Proximal end of internode bluntly tapering, formed by 2 opposing zooecia narrower than more distal ones. One simple, terminal opening occurs at proximal end of each of the 2 proximal zooecia. Distal end of internode not well preserved.

Zooecia club-shaped, separated by furrows ; length nearly twice width. Gymnocyst about half zooecial length, arched, smooth, developed proximally only, covered in all but the proximal zooecia by enlarged avicularian chambers. Cryptocyst imperforate, smooth, well developed but narrow, horse-shoe shaped, limited to proximal and lateral margins ; not widened proximally. Surface of cryptocyst a smooth, horizontal shelf.

Opesia oval, more broadly rounded proximally, with a narrow shelf, lower than the cryptocyst, developed distally.

Avicularia adventitious, paired, with enlarged chambers meeting on mid-line of proximal gymnocyst and curving distally and outwards to open on disto-lateral margins of opesiae of adjoining rows. Rostrum short, pointed, directed proximally. Pivotal bar complete. Chamber with a distinct proximal pore.

Ovicell unknown.

MEASUREMENTS :

Lz (3) 0·581 (0·0226) mm., 0·56–0·60 mm.
lz (3) 0·319 (0·0522) mm., 0·27–0·38 mm.
ho (3) 0·359 (0·0171) mm., 0·34–0·38 mm.
lo (3) 0·185 (0·0430) mm., 0·14–0·23 mm.
Lav (4) 0·090 (0·0086) mm., 0·09–0·10 mm.

REMARKS. This species resembles *N. appendiculata* (Hincks) (Department of Zoology, British Museum (Natural History), 99.5.1.506, Hincks Collection) and *N. tenuis* Harmer (holotype, Department of Zoology, B.M. (N.H.), 28.3.6.62, Siboga Collection), Recent Indo-Pacific species, in zooecial size and shape, zoarial articulation, and avicularian size, shape, and position. Moreover, it appears to agree with *N. appendiculata* in having short, stubby internodes. Neither of the Recent species, however, has the avicularian chambers so enlarged as to meet over the proximal gymnocyst as they do in *N. ventricosa*, and further in both of those species the cryptocyst widens proximally. Harmer (1926 : 246) deemed differences of this magnitude sufficient to separate the two Recent species, so *N. ventricosa* should probably be maintained as a separate species.

N. midwayanica Canu & Bassler (1920 : 197, pl. 4, figs. 10–15), from the Palaeocene of the Gulf Coast of the U.S.A., differs from *N. ventricosa* in having longer internodes, less-developed avicularian chambers, and no distal shelf.

DISTRIBUTION. Eocene (Lutetian) ; France, ?Senegal.

Genus ***VINCULARIA*** Defrance

1829 *Vincularia* Defrance : 214.
1907*b* *Heterocella* Canu : 70 (objective).

TYPE SPECIES (by monotypy). *Vincularia fragilis* Defrance 1829 : 214, pl. 45, figs. 3, 3*a*, *b*. Eocene (Lutetian) ; vicinity of Paris, France.

DIAGNOSIS. Zoarium erect, probably articulated, the internodes quadriserial, slender, with 3 openings in each proximal end and 6 in each distal end. Zooecia dimorphic or trimorphic, similar zooecia occurring in 2 adjacent series : (1) *ordinary zooecia* (= " c-zooecia " of Canu 1907*b* : 71) small, with symmetrical opesiae ; (2) *avicularian* (?) *zooecia* (= " D-zooecia " of Canu) usually larger, with asymmetrical opesiae, outwardly curving distal margins, and usually distinct distal cryptocystal shelves ; and (3) *ovicelled zooecia* (lacking in some species) large, with symmetrical opesiae surmounted by the entozooecial ovicells. Zooecia of all three types with membranous frontal wall, lacking gymnocyst. Cryptocyst a narrow, imperforate shelf round lateral and proximal margins of the large, oval opesia. Communication between zooecia of the same series by a large, median septule ; between zooecia of adjacent series by a septule connecting disto-lateral wall of one with proximo-lateral wall of the other. Small, single, adventitious avicularium present on mural rim of some species.

REMARKS. Brown (1952 : 90, 91) remarked on the nomenclatorial inconsistency of declaring *Vincularia* an unrecognizable name while retaining its absolute junior synonym, *Heterocella* Canu (see Bassler 1935 : 125, 225).

The genus *Vincularia* apparently ranges from Middle to Upper Eocene (Lutetian, Auversian, Bartonian) both in England and on the Continent. It is yet unknown from America or, with certainty, from strata of Oligocene age. *Heterocella vicksburgica* Canu & Bassler (1920 : 198, pl. 82, figs. 11–14), from the Oligocene of Alabama, U.S.A. ; *Vincularia hians* Reuss and *V. haidingeri* Reuss (Kyri 1951 : 74, 75), from the Eocene (Ludian) of Rumania ; *Heterocella lerichei* Canu (1907*a* : 512, pl. 12, fig. 2), from the Oligocene (Stampian) and Miocene (Aquitanian) of France ; and *Heterocella pentagona* Canu & Bassler (1929*b* : 111, pl. 9, figs. 13–16), from the western Pacific, do not appear to have the avicularian (?) or " D " zooecia characteristic of the genus. Dartevelle (1942 : 149) stated that *Glauconome tetragona* Münster is " an undoubted " *Vincularia* but gave no evidence to support his claim. The six species included in the following table are the only ones which can at present be placed in the genus with certainty.

KEY TO SPECIES OF *VINCULARIA*

(Species named in square brackets are not described here.)

1 Zooecia trimorphic ; ovicelled zooecia present 2
  Zooecia dimorphic ; ovicelled zooecia absent 4
2 Ovicelled zooecia greatly enlarged ; avicularian zooecia separated by a thread ; adventitious avicularia on zooecia of all three types . . ***V. monstruosa*** (Canu)
  Ovicelled zooecia subequal to ordinary zooecia ; avicularian zooecia separated by a groove 3
3 Adventitious avicularia on ordinary and ovicelled zooecia only [***V. polymorpha*** (Canu)]
  Adventitious avicularia on zooecia of all three types . . [***V. lediensis*** (Dartevelle)]
4 Adventitious avicularia present ; avicularian zooecia curved outwards strongly [***V. fragilis*** Defrance]
  Adventitious avicularia absent ; avicularian zooecia curved outwards only slightly 5
5 Zooecia of both types slender, with elongate cryptocyst . . . ***V. davisi*** sp. nov.
  Zooecia of both types obese, with short cryptocyst . . [***V. subsymmetrica*** (Canu)]

1. ***Vincularia monstruosa*** (Canu)

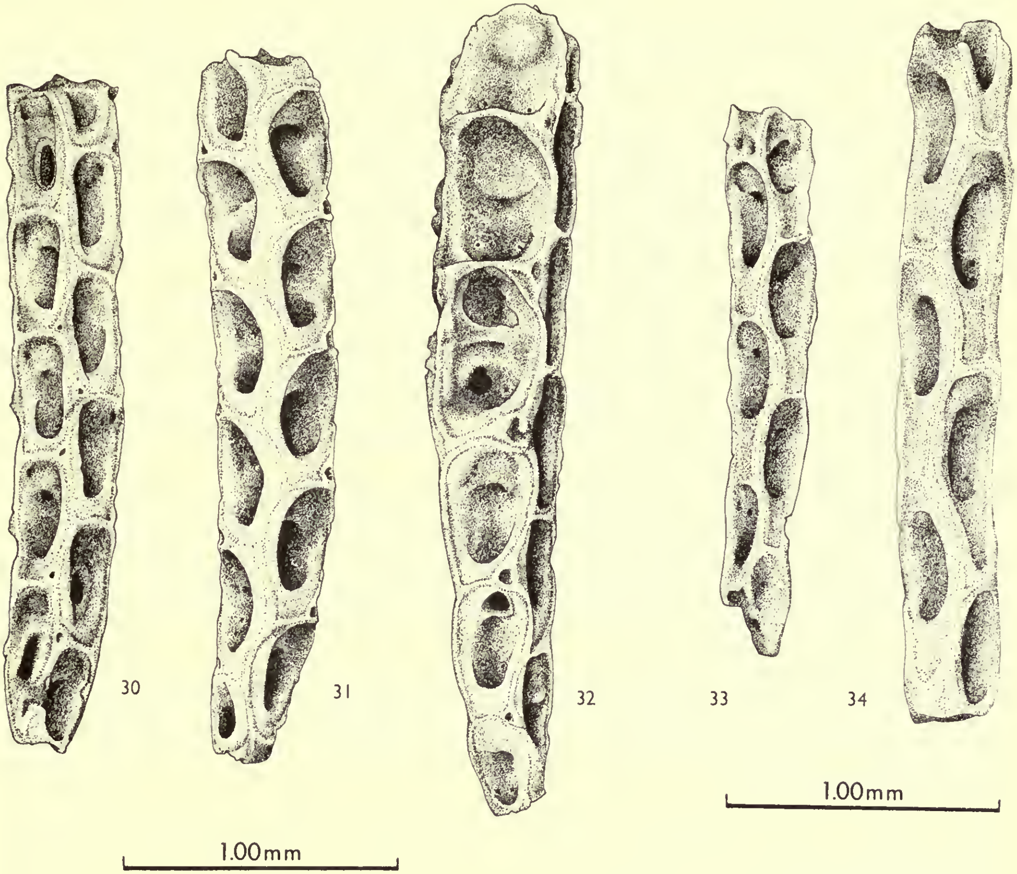
(Text-figs. 30–32)

1907*b* *Heterocella monstruosa* Canu : 71, pl. 10, figs. 11, 12.
1946 *Heterocella monstruosa* Canu : Buge : 430.
1956 *Vincularia monstruosa* (Canu) Balavoine : 324.
1960 *Vincularia monstruosa* (Canu) ; Balavoine : 246.
?1962 *Heterocella* sp., Davis : 194.

FIGURED SPECIMENS. D.48533 (Text-fig. 30), D.48534 (Text-fig. 31), D.48535 (Text-fig. 32).

ADDITIONAL MATERIAL. Ninety-one specimens, D.48536–D.48626.

DIAGNOSIS. *Vincularia* with trimorphic zooecia, the avicularian (?) ones curving away from each other markedly and separated by a thread ; ordinary and avicularian (?) zooecia both with very short cryptocysts ; adventitious avicularia at inner proximo-lateral angle of ordinary zooecia and at outer proximo-lateral angle of



FIGS. 30–34. Fig. 30. *Vincularia monstruosa* (Canu). D.48533. Internode fragment showing the two series of ordinary zooecia. Fig. 31. *Vincularia monstruosa* (Canu). D.48534. Internode fragment showing the two series of avicularian (?) zooecia. Fig. 32. *Vincularia monstruosa* (Canu). D.48535. Internode fragment showing a series of three avicularian (?) zooecia giving rise to a series of three ovicelled zooecia. Fig. 33. *Vincularia davisi* sp. nov. D.48627. Holotype. Internode fragment showing the two series of ordinary zooecia. The distal zooecium on the left has a pair of pores possibly associated with articulation. Fig. 34. *Vincularia davisi* sp. nov. D.48628. Paratype. Internode fragment showing the two series of avicularian (?) zooecia.

avicularian (?) and ovicelled zooecia ; ovicelled zooecia greatly enlarged, with well-developed entozooecial ovicells.

Description. *Zoarium* erect, probably articulated, composed of long, slender, curved internodes, tapering towards the base, lozenge-shaped in cross-section, the faces separated by obtuse angles having similar zooecia. Zooecia of adjacent rows alternate in position. Length of internode at least 7 zooecia. Proximal end of internode with 3 openings, 2 in avicularian (?) zooecia, 1 in ordinary zooecium. Distal end of internode with 6 openings, 2 in each of 2 avicularian (?) zooecia, 1 in each of 2 ordinary zooecia.

Ordinary zooecia rounded rectangular, separated by their narrow, smooth, rounded mural rims. Length about twice width. Interior very shallow, with a large, circular septule centrally, 2 similar ones disto-laterally, and 2 smaller ones near middle of lateral walls. Cryptocyst smooth, imperforate, slightly concave, forming a narrow, crescent-shaped shelf proximally and laterally. A similar, but deeper shelf runs distally from central septule to distal mural rim, sometimes connecting with the proximal cryptocyst to form a closure. Opesia oval, more broadly rounded distally than proximally, without differentiated indentations.

Avicularian (?) zooecia asymmetrically club-shaped, the longitudinal axes of those in one series curving strongly away from those of the other. Zooecia of both series separated by their narrow, smooth, rounded mural rims which are narrowest at the outer distal corner. Zooecial length twice width. Interior with same appearance and arrangement of pores as ordinary zooecia. Cryptocyst as in ordinary zooecia. Opesia as in ordinary zooecia but asymmetrical.

Ovicelled zooecia occur at distal end of series of avicularian (?) zooecia, rounded rectangular, larger than zooecia of other types, separated by narrow, rounded, smooth mural rims. Length slightly greater than width. Cryptocyst greatly reduced. Interior as in ordinary zooecia, except at distal end where distal wall is concave and slightly elevated, forming an entozooecial ovicell which extends slightly under cryptocyst of distal zooecium.

Avicularia adventitious, very small, single, placed proximo-laterally on mural rim with rounded rostrum directed distally and outwards. Ordinary zooecia with avicularium at inner proximal angle ; zooecia of other two types with avicularium at outer proximal angle.

Measurements :

Ordinary zooecia

Lz	(9)	0·440 (0·0350) mm., 0·36–0·47 mm.
lz	(10)	0·206 (0·0219) mm., 0·17–0·23 mm.
ho	(8)	0·346 (0·0330) mm., 0·27–0·38 mm.
lo	(10)	0·141 (0·0092) mm., 0·13–0·15 mm.
Lav	(9)	0·056 (0·0128) mm., 0·04–0·08 mm.

Avicularian (?) zooecia

Lz (10) 0·471 (0·0311) mm., 0·41–0·53 mm.
lz (9) 0·278 (0·0196) mm., 0·26–0·32 mm.
ho (10) 0·362 (0·0214) mm., 0·34–0·41 mm.
lo (9) 0·176 (0·0284) mm., 0·13–0·21 mm.
Lav (6) 0·078 (0·0084) mm., 0·07–0·09 mm.

Ovicelled zooecia

Lz (3) 0·522 (0·1150) mm., 0·39–0·61 mm.
lz (2) 0·415 (0·0191) mm., 0·40–0·43 mm.
ho (3) 0·504 (0·0964) mm., 0·39–0·56 mm.
Lav (1) 0·09 mm.

REMARKS. It is very likely that this abundant Upper Bracklesham species is the one which Davis (1962 : 194) identified from Selsey as *Heterocella* sp.

DISTRIBUTION. Eocene (Lutetian) ; France. ?Eocene (Auversian) ; England.

2. ***Vincularia davisi***[8] sp. nov.

(Text-figs. 33, 34)

HOLOTYPE. D.48627 (Text-fig. 33).

PARATYPES. D.48628 (Text-fig. 34), D.48629–D.48640 (12 specimens), and L.S.U. 8034.

DIAGNOSIS. *Vincularia* with dimorphic zooecia, the avicularian (?) ones curving away from each other only slightly so that they are not much different in form from the ordinary ones ; avicularian (?) zooecia separated by threads ; ordinary zooecia with very elongate proximal cryptocyst ; adventitious avicularia and ovicells lacking.

DESCRIPTION. *Zoarium* erect, probably articulated, composed of long, very slender internodes, nearly square in cross-section ; similar zooecia occur in each of the two adjacent series, alternating in position. Articulating ends of internodes not preserved.

Ordinary zooecia club-shaped, nearly three times as long as wide, separated by contiguous, broad, smooth, rounded mural rims. Interior shallow, with a large, circular, distal-median septule flanked on either side by a smaller one. Cryptocyst smooth, imperforate, slightly concave, forming a long shelf proximally and a very narrow one on each lateral margin. Distal wall without distinct shelf. Closures formed by proximal growth of a lamina from distal mural rim. Opesia oval, more broadly rounded distally than proximally, without opesiular indentations.

Avicularian (?) zooecia club-shaped, only slightly asymmetrical, the longitudinal axes of those in one series curving just perceptibly away from those in the other. Zooecia of the two series separated by their contiguous, smooth, rounded mural rims.

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[8] After the late A. G. Davis.

Zooecial length two and a half times width. Septules as in ordinary zooecia. Cryptocyst as in ordinary zooecia, but wider laterally and continuing round distal margin of opesia in a broad shelf. Opesia oval, nearly symmetrical.

Adventitious *avicularia* and *ovicell* lacking.

MEASUREMENTS :

Ordinary zooecia

Lz (7) 0·602 (0·0517) mm., 0·56–0·70 mm.
lz (7) 0·211 (0·0128) mm., 0·19–0·23 mm.
ho (7) 0·372 (0·0119) mm., 0·36–0·39 mm.
lo (7) 0·130 (0·0134) mm., 0·11–0·15 mm.

Avicularian (?) zooecia

Lz (6) 0·789 (0·0515) mm., 0·70–0·85 mm.
lz (7) 0·300 (0·0277) mm., 0·26–0·32 mm.
ho (6) 0·370 (0·0467) mm., 0·31–0·43 mm.
lo (7) 0·145 (0·0131) mm., 0·13–0·17 mm.

REMARKS. This species is most closely related to the French Lutetian *V. subsymmetrica* (Canu) which it resembles in having dimorphic zooecia with the avicularian (?) zooecia only slightly curved and in lacking adventitious avicularia. The zooecia of *V. subsymmetrica* contrast with those of *V. davisi* in being obese and in having short cryptocysts.

Suborder ACANTHOSTEGA

Family **CRIBRILINIDAE** Hincks

Genus ***CRIBRILARIA*** Canu & Bassler

Cribrilaria parisiensis (Canu)

(Text-figs. 35, 36)

1913 " *Cribrilina puncturata* Busk " ; Canu : 148, pl. 4, fig. 3.
1926 *Cribrilina parisiensis* Canu : 751, pl. 27, fig. 1 ; pl. 29, fig. 6.
1929*a* *Cribrilina parisiensis* Canu ; Canu & Bassler : 37.
1933 *Cribrilina parisiensis* Canu ; Dartevelle : 106.
1936 *Cribrilina parisiensis* Canu ; Dartevelle : 29.
1954 *Cribrilina parisiensis* Canu ; Balavoine : 256.

FIGURED SPECIMEN. D.48641 (Text-figs. 35, 36).

ADDITIONAL MATERIAL. Four specimens, D.48642–D.48645.

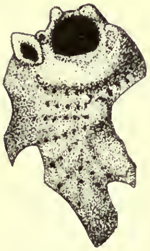
DIAGNOSIS. *Cribrilaria* with paired adventitious avicularia and without distinct lumen pores ; ovicell without rim ; ovicelled zooecia without oral spines.

DESCRIPTION. *Zoarium* encrusting, unilaminar, the zooecia arranged in irregular longitudinal rows increasing in number distally by bifurcation. Zooecia in adjacent rows alternate in position.

Zooecia elliptical, separated by distinct grooves. Length about one and a half times width. Frontal shield convex, highest at sub-oral umbo, without definite gymnocyst. Costae 8–11 excluding apertural bar, narrow, smooth, tapering towards centre of shield, without distinct lumen pores. Lacunae small, circular or elliptical, 6 or rarely 5 between adjacent costae. Apertural bar about half as wide again as costae, not tapering, strongly curved, with a projecting, central umbo which is concave on both distal and proximal sides.

Orifice terminal on frontal surface, small, semi-circular, the proximal lip slightly concave. Distal margin with 4 erect, hollow spine bases (lacking in ovicelled zooecia).

Avicularia adventitious, small, paired, frontal, placed one on either side of orifice, the rostrum directed distally and outwards. Rostrum short, pointed. Complete pivotal bar sometimes preserved.



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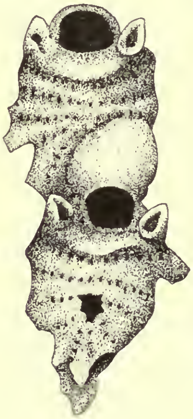

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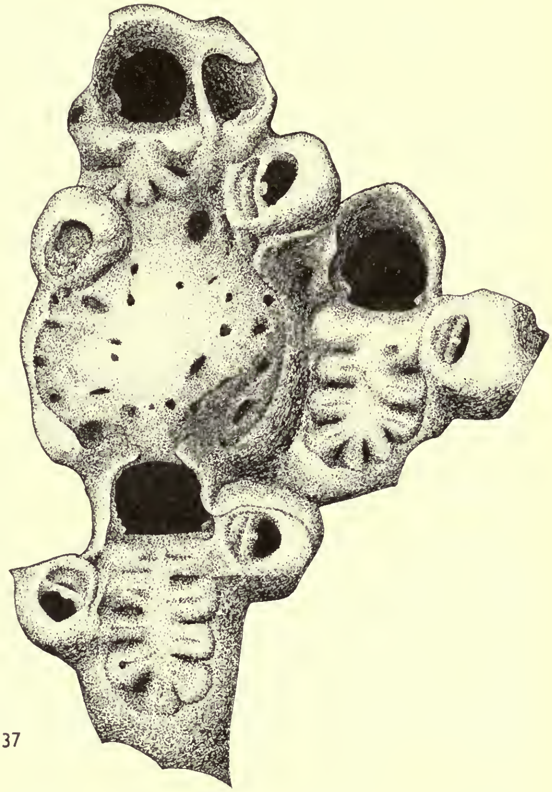

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Figs. 35–37. Figs. 35, 36. *Cribrilaria parisiensis* (Canu). D.48641. A non-ovicelled zooecium and two other zooecia, the proximal one ovicelled, in different parts of the same fragmentary zoarium. Fig. 37. *Membraniporella radiata* (Reuss). D.48646. Three zooecia, the proximal one ovicelled.

Ovicell hyperstomial, globular, nearly circular in frontal outline. Surface smooth, imperforate, without rim. Opening nearly perpendicular to zooecial orifice, small, semi-circular.

MEASUREMENTS :

Lz (8) 0·316 (0·0183) mm., 0·30–0·34 mm.
lz (8) 0·252 (0·0323) mm., 0·20–0·30 mm.
ho (9) 0·057 (0·0060) mm., 0·05–0·07 mm.
lo (9) 0·092 (0·0071) mm., 0·09–0·10 mm.
Lav (7) 0·055 (0·0068) mm., 0·05–0·07 mm.
Lov (6) 0·140 (0·0070) mm., 0·13–0·14 mm.

REMARKS. This species does not fit easily in any known Cribrilinid genus. The frontal shield, including the absence of a gymnocyst, the orifice, and the ovicell are very much like those of *Eschara radiata* Moll, the type species of *Cribrilaria*, which has vicarious, rather than adventitious avicularia.[9] The avicularia of *C. parisiensis* are quite like those of *Lepralia gattyae* Busk, the type species of *Puellina*, which has a different frontal shield. By analogy with other Acanthostega, e.g. *Castanopora* (see Larwood 1962 : 203–206), greater systematic weight is placed on the form of the frontal shield than on the position of the avicularia.

C. parisiensis differs from the eastern European Upper Eocene species, *C. calomorpha* (Reuss), in number of costae and form of orifice (see Malecki 1963 : 115).

DISTRIBUTION. Eocene (Auversian) ; Belgium, France. Eocene (Bartonian) ; Belgium. Oligocene (Stampian) ; France.

Genus ***MEMBRANIPORELLA*** Smitt

1873 *Membraniporella* Smitt : 10.

TYPE SPECIES (selected by Hincks 1877). *Lepralia nitida* Johnston 1838 : 277, pl. 34, fig. 7. Recent ; British Isles.

DIAGNOSIS. Frontal shield composed of relatively few costae over-arching a well-developed membrane. Gymnocyst prominent proximally and laterally. Costae usually with conspicuous, open lumina. Lacunae slit-like and undivided or with few lateral fusions. Orifice semi-circular to sub-circular, sometimes with lateral condyles. Distal spines frequently present. Avicularia, where present, adventitious, placed usually on proximal part of gymnocyst near orifice of laterally adjacent zooecium. Ovicell hyperstomial, imperforate in the type species, elongate globular. Orifice of ovicelled zooecia slightly wider than that of non-ovicelled ones.

REMARKS. Though the diagnosis given here is based in large part on the type species, *L. nitida* (holotype, Department of Zoology, British Museum (Natural History), 47.9.16.66, Johnston Collection), it has been framed to embrace the extremes of variation shown by *M. aragoi* (Audouin) (see Harmer 1926, pl. 34, figs. 12–14) and *M. compressa* Canu & Bassler (1920, pl. 41, figs. 6–8). Such species as *M. radiata* (Reuss), described below, and *M. planula* Canu & Bassler (1920, pl. 5, figs. 8–10), *M. ulrichi* Canu & Bassler (1920, pl. 41, figs. 4, 5), *M. monilifera* Canu & Bassler (1920, pl. 41, figs. 9, 10), *M. bioculata* Canu & Bassler (1920, pl. 41, figs. 11–13), and *M.*? *subagassizi* Canu & Bassler (1920, pl. 84, figs. 8–13) seem to be much closer to the type species.

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[9] *C. calomorpha* (Reuss) (Malecki 1963 : 115), from the Ludian of Poland and Rumania, also has paired adventitious avicularia ; *C. simulator* (Canu & Bassler 1920 : 298, pl. 41, fig. 21 ; pl. 84, fig. 14), from the Upper Eocene and Oligocene of the Gulf Coast of the U.S.A., has paired adventitious avicularia on the ovicelled, but not the ordinary zooecia.

Membraniporella radiata (Reuss)

(Text-fig. 37)

1869*a* *Celleporaria radiata* Reuss : 292, pl. 30, fig. 9.
1885 *Cribrilina chelys* Koschinsky : 36.
1889 *Cribrilina chelys* Koschinsky ; Pergens : 70.
1891 *Cribrilina chelys* Koschinsky ; Waters : 16, pl. 2, fig. 10.
1898 *Cribrilina chelys* Koschinsky ; Neviani : 39, text-fig. 1.
1907*b* *Cribrilina chelys* Koschinsky ; Canu : 145, pl. 20, fig. 1.
1929*a* *Collarina radiata* (Reuss) Canu & Bassler : 34, pl. 2, figs. 17, 18.
1933 *Collarina radiata* (Reuss) ; Dartevelle : 101.
1946 *Cribrilina chelys* Koschinsky ; Buge : 433.
1951 *Collarina radiata* (Reuss) ; Kyri : 74.
1962 *Collarina radiata* (Reuss) ; Ghiurca, table 1.

FIGURED SPECIMEN. D.48646 (Text-fig. 37).

ADDITIONAL MATERIAL. Three specimens, D.48647–D.48649.

DIAGNOSIS. *Membraniporella* with 5–7 costae in addition to the apertural bar and without lateral fusions ; costae with exposed, slit-like lumina ; orifice with lateral condyles ; avicularia adventitious, single, paired, or multiple on the lateral gymnocyst and, occasionally, vicarious as well ; ovicell large, coarsely perforate.

DESCRIPTION. *Zoarium* erect, bilaminar, compressed, the zooecia arranged in irregular, alternating, longitudinal rows.

Zooecia irregularly elliptical, nearly twice as long as wide, separated by furrows. Gymnocyst wide, especially proximally, strongly arched, smooth. Frontal shield relatively flat, small, barely twice the size of the orifice. Costae 5–7 (usually 7) excluding apertural bar, short, broad, triangular, smooth, each with a single, slit-like, exposed lumen. Adjacent costae without lateral fusions, separated by a single, slit-like lacuna. Median line of shield with thin, smooth, irregular ridge formed by fusion of ends of costae. Apertural bar formed by a pair of opposing costae slightly thicker than the others.

Orifice sub-circular, less rounded proximally than distally, with a pair of stout, deeply placed lateral condyles close to proximal margin. Peristome short, thin, present distally only. Oral spines lacking.

Avicularia adventitious, single, paired, or, rarely, multiple, placed on lateral gymnocyst proximal to orifice in such position as to be near orifice of zooecium of adjacent row. Rostrum umbo-like, rounded, directed upwards, outwards, and slightly distally or proximally. Pivotal bar complete, with small, rounded knob on rostral side.

Vicarious avicularia lacking in specimens at hand.

Ovicell hyperstomial, larger than zooecia, globular, with coarsely perforate surface. Orifice of ovicelled zooecia semi-circular, wider than that of ordinary zooecia, with weaker condyles and better-developed distal peristome.

MEASUREMENTS :

Ordinary zooecia

Lz (5) 0·575 (0·0237) mm., 0·56–0·62 mm.
lz (6) 0·304 (0·0438) mm., 0·23–0·34 mm.
ho (5) 0·147 (0·0140) mm., 0·14–0·17 mm.
lo (6) 0·144 (0·0183) mm., 0·13–0·17 mm.
Lav (7) 0·171 (0·0086) mm., 0·16–0·19 mm.

Ovicelled zooecia

lo (5) 0·190 (0·0164) mm., 0·17–0·21 mm.
Lov (5) 0·498 (0·0299) mm., 0·44–0·51 mm.

DISTRIBUTION. Eocene (Lutetian) ; France, Germany. Eocene (Auversian) ; Belgium. Eocene (Ludian) ; Poland, Italy, Rumania.

Suborder ASCOPHORA

Family **EXECHONELLIDAE** Harmer

Genus ***EXECHONELLA*** Duvergier

1924 *Exechonella* Duvergier : 18.

TYPE SPECIES (by monotypy). *Cyclicopora*? *grandis* Duvergier 1921 : 124, pl. 3, figs. 2, 3. Miocene (Aquitanian) ; Gironde, France.

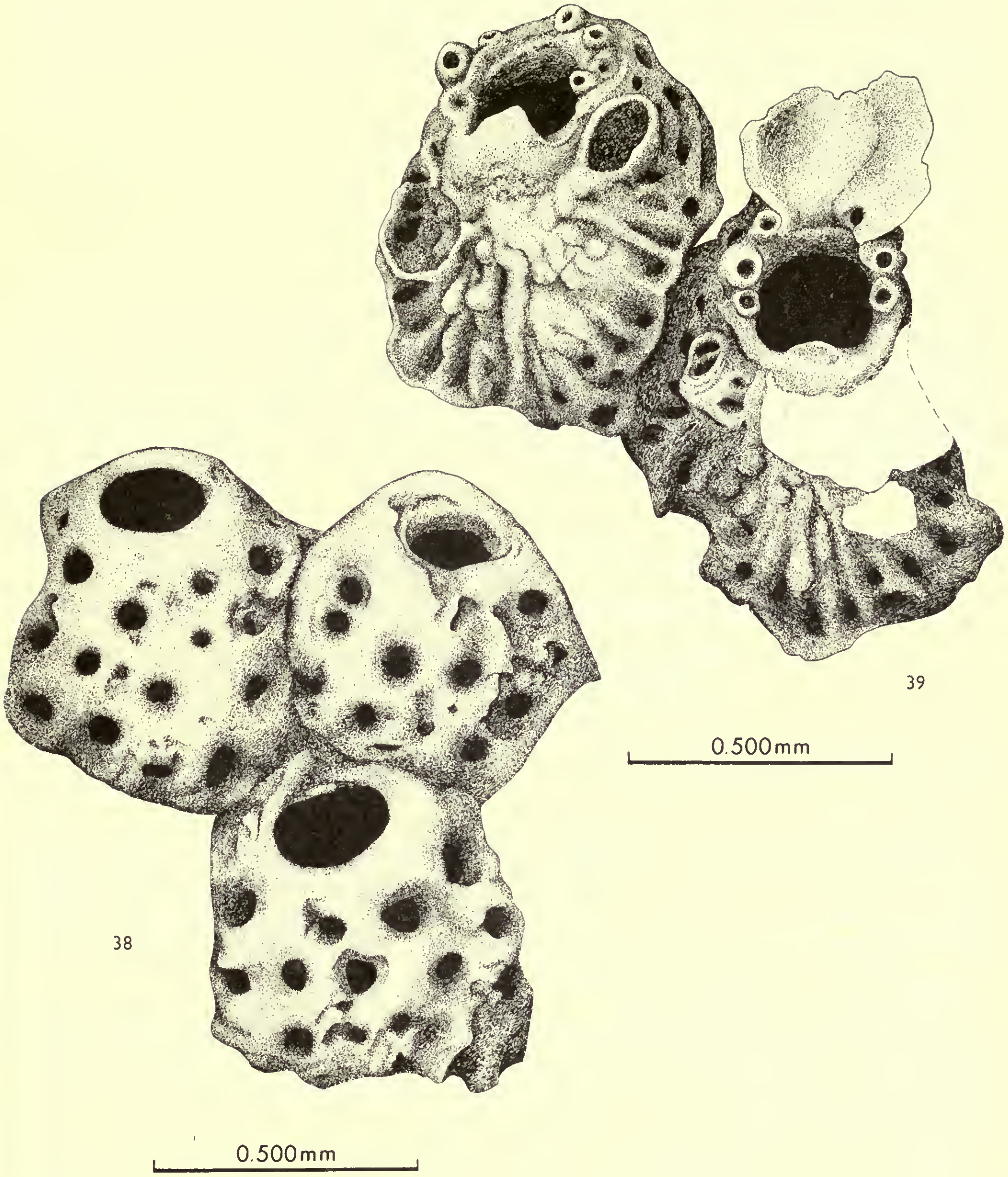
DIAGNOSIS. Frontal wall calcareous, over-arching a fully developed membrane. Frontal pores large, irregularly dispersed over surface, not filled with tissue. Peristome long or short, tubular, with small lateral denticles or none. Secondary orifice sub-circular. Avicularia, where present, adventitious, frontal, with pointed rostrum and pivotal bar. Ovicells usually lacking ; where present, small, developed on distal side of peristome.

REMARKS. This genus is usually attributed to Canu & Bassler (1927 : 4), who selected as type species *Hiantopora magna* MacGillivray (see Harmer 1957 : 652). However irregular, Duvergier's introduction of the genus has priority, with *C.*? *grandis* the type species by monotypy.

Exechonella sp.

(Text-fig. 38)

FIGURED SPECIMEN. D.48650 (Text-fig. 38).



Figs. 38–39. Fig. 38. *Exechonella* sp. D.48650. Three zooecia from the small zoarial fragment. Fig. 39. *Hippopleurifera canui* nom. nov. D.48651. Two zooecia, the one on the right ovicelled, from the small zoarial fragment.

Description. *Zoarium* presumably encrusting, the basal surface uncalcified.

Zooecia irregularly elliptical, separated by shallow, poorly defined grooves. Length and width subequal. Frontal wall strongly inflated, thick, smooth, with 12–15 large, circular, quincuncially arranged foramina.

Peristome short, the secondary orifice terminal on frontal surface, sub-circular, slightly wider than long, without denticles.

Avicularia and *ovicells* lacking in specimen at hand.

Measurements :

Lz	(4) 0·614 (0·0237) mm., 0·55–0·68 mm.	
lz	(4) 0·603 (0·0386) mm., 0·56–0·65 mm.	
ho	(4) 0·141 (0·0164) mm., 0·12–0·15 mm.	secondary orifice
lo	(4) 0·214 (0·0209) mm., 0·19–0·24 mm.	

Remarks. Only one fragment, badly worn and consisting of just 7 zooecia, recovered from the Upper Bracklesham material, is referable to *Exechonella*. Absence of positive characters, probably a consequence of its poor preservation, makes specific assignment impossible.

Family **UMBONULIDAE** Canu

Genus ***HIPPOPLEURIFERA*** Canu & Bassler

Hippopleurifera canui[10] nom. nov.

(Text-fig. 39)

1873 *non Hippothoa mucronata* Smitt : 45, pl. 8, fig. 169.
1914*a* *Petralia mucronata* Canu : 301, pl. 4, fig. 5 (misspelt " *micronata* ").

Figured specimen. D.48651 (Text-fig. 39).

Diagnosis. Unilaminar, probably encrusting *Hippopleurifera*, with large, mucronate zooecia ; areolae in a single row ; orifice with feeble condyles and 6 distal spines on non-ovicelled and 4–6 on ovicelled zooecia ; avicularium single or paired, lateral sub-oral, with rostrum directed proximally and inwards.

Description. *Zoarium* unilaminar, probably encrusting.

Zooecia rhomboidal, separated by a shallow groove. Length nearly one and a half times width. Frontal wall thick, very convex, highest at mucro. Surface coarsely tuberculate centrally, areolate in a single row marginally, with inter-areolar costules nearly reaching centre.

Orifice large, terminal, inclined distally, hidden by a large, projecting mucro proximally, rounded sub-quadrate, with a pair of feeble condyles near proximal corners of lateral margins. Distal margin with 6 large, hollow spine bases on both ovicelled and non-ovicelled zooecia, in material at hand.

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[10] After the late Ferdinand Canu.

Avicularium adventitious, frontal, single in material at hand, placed near proximo-lateral margin of orifice with rostrum directed upwards, proximally, and slightly inwards. Rostrum rounded, pivotal bar complete.

Ovicell hyperstomial, globular, elongate. Surface not preserved in specimen at hand.

MEASUREMENTS :

Lz	(2) 0·821	(0·0242) mm.,	0·80–0·84 mm.
lz	(2) 0·611	(0·0181) mm.,	0·60–0·62 mm.
ho	(2) 0·222	(0·0121) mm.,	0·21–0·23 mm.
lo	(2) 0·214	(0·0242) mm.,	0·20–0·23 mm.

REMARKS. Canu (1914*a* : 301) described the ovicell of this species as having crescents incompletely calcified on their edges, but in his figure (pl. 4, fig. 5) the surface of the ovicell appears smooth. The specimen illustrated by Canu has 4 spines on the ovicelled zooecia in contrast to the 6 (one overlapped by the floor of the ovicell) displayed by the Upper Bracklesham specimen. Canu characterized the species as having paired avicularia, but his figure shows only one zooecium with two avicularia. One of the zooecia in the Upper Bracklesham specimen may have a small remnant of a second avicularium.

This species is represented in the Curry Collection by the single specimen of two almost complete and one fragmentary zooecia.

DISTRIBUTION. Eocene (Lutetian) ; France.

Family **EXOCHELLIDAE** Bassler

Genus ***ESCHAROIDES*** Milne Edwards

1836 *Escharoides* Milne Edwards : 218.
1902 *Peristomella* Levinsen : 26.

TYPE SPECIES (chosen by Norman 1903). *Cellepora coccinea* Abildgaard 1806 : 30, pl. 146, figs. 1, 2. Recent ; North Sea, Heligoland.

DIAGNOSIS. Frontal wall calcareous, granular to tuberculate, with a single row of marginal areolae separated by short, peripheral costules. Orifice sub-circular, deeply buried in peristome, steeply inclined distally, with a short, curved plate projecting into the zooecium from its distal margin. Peristome not differentiated from frontal surface, sometimes with distal spines. Secondary orifice oval, usually with a median-proximal denticle, and sometimes with a pair of proximo-lateral ones as well. Avicularia adventitious, usually paired, placed on lateral margins of frontal near proximal part of peristome. Rostrum usually pointed, directed outwards and distally. Pivotal bar complete. Larger, vicarious avicularia, with swollen chamber margined with areolae, sometimes present. Ovicell hyperstomial, globular, with marginal areolae separated by costules, and, at least in some species, with finer perforations in radial lines between costules. Interzooecial communication by pore-chambers. Operculum a weakly chitinized valve.

REMARKS. Brown's suggestion (1952 : 298) that species of *Escharoides* with well-developed marginal areolae on the ovicells may have to be transferred to a new genus need not be followed, for specimens of the type species (e.g. Department of Zoology, British Museum (Natural History), 99.5.1.858, 91.8.7.16, 93.8.7.31, and 1950.11.6.4) show ovicells with distinct areolae. Most species of *Escharoides* have pointed, not spatulate avicularia (cf. Brown 1952 : 297).

Escharoides aliferus (Reuss)

(Text-figs. 40, 41)

1869*a* *Eschara alifera* Reuss : 274, pl. 33, fig. 11.
1887 *Eschara alifera* Reuss ; Pergens : 7.
1889 *Mucronella alifera* (Reuss) Pergens : 71.
1891 *Smittia coccinea* var. *alifera* (Reuss) ; Waters : 21, pl. 3, fig. 7.
1908 *Peristomella alifera* (Reuss) Canu : 92, pl. 7, fig. 7.
1925 *Peristomella alifera* (Reuss) ; Canu : 47.
1946 *Escharoides aliferus* (Reuss) Buge : 434.
1949 *Peristomella alifera* (Reuss) ; Balavoine : 774.
1957 *Escharoides aliferus* (Reuss) ; Balavoine : 191.
1960 *Romancheina gouetensis* Balavoine : 247, pl. 6, figs. 11–14 ; pl. 7, figs. 1–4.
1962 *Escharoides aliferus* (Reuss) ; Ghiurca, table 1.
1963 *Escharoides aliferus* (Reuss) ; Braga : 34.

FIGURED SPECIMENS. D.48652 (Text-fig. 40), D.48653 (Text-fig. 41).

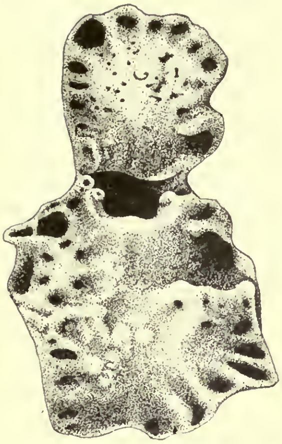
ADDITIONAL MATERIAL. Twenty-two specimens, D.48654–D.48675.

DIAGNOSIS. Erect, bilaminar *Escharoides* with prominent mucro flanked by a smaller denticle on either side ; a single spine base at each lateral margin of secondary orifice ; avicularia paired, occupying swollen chambers at lateral margins of frontal ; ovicell elongate, irregularly perforated, areolated.

DESCRIPTION. *Zoarium* erect, arborescent, arising from an encrusting base, composed of compressed, bilaminar fronds with more than 12 longitudinal rows of zooecia on each side ; the zooecia in adjacent rows alternate in position. Interzooecial communication by small pore-chambers in distal and disto-lateral walls.

Zooecia irregularly rhombic, rounded distally, the lateral avicularia forming wing-like expansions on the sides. Zooecia separated by shallow, ill-defined depressions. Zooecial length almost one and a half times width. Frontal wall moderately thick, convex, highest at proximal lip of secondary orifice. Surface smooth except for

FIGS. 40–47. Fig. 40. *Escharoides aliferus* (Reuss). D.48652. Ovicelled zooecium. Fig. 41. *Escharoides aliferus* (Reuss). D.48653. Two non-ovicelled zooecia. Fig. 42. *Smittoidea variabilis* (Canu). D.48676. Two zooecia from a bilaminar fragment. The one on the right has an avicularium. Fig. 43. *Smittoidea variabilis* (Canu). D.48677. A zooecium from another bilaminar fragment in a more advanced state of calcification. Fig. 44. *Smittoidea variabilis* (Canu). D.48678. An ovicelled zooecium from a unilaminar fragment. Fig. 45. *Smittoidea variabilis* (Canu). D.48679. An ovicelled zooecium from another unilaminar fragment. The peristome is unusually developed. Figs. 46, 47. *Smittoidea variabilis* (Canu). D.48679. A zooecium and the outline of an avicularium of another zooecium from the same unilaminar fragment.



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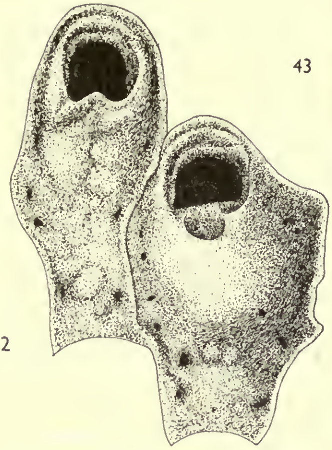

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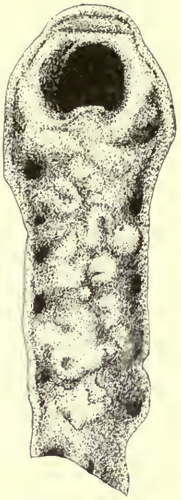

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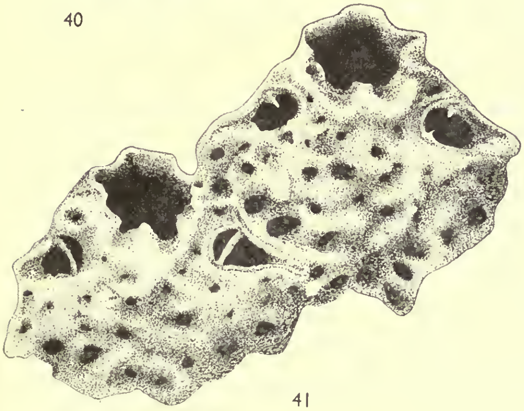

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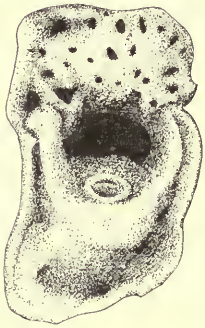

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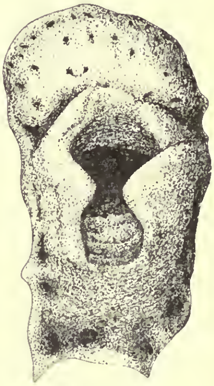

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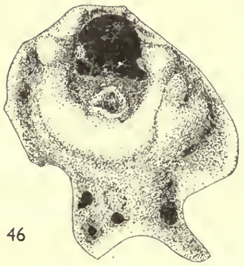

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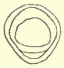


47

0.500 mm

large, irregular tubercles along mid-line and prominent peripheral costules separating the areolae. Areolae large, sub-circular or elliptical, evenly spaced in a row of 18–25 round lateral and proximal margins. Additional, smaller areolae, 4–6, on line separating avicularian chamber from frontal surface.

Orifice small, sub-circular, inclined distally, deeply buried in peristome. Distal plate well developed, with straight margin and concave surface. Peristome not differentiated from frontal surface, thin, with a small, hollow spine base at mid-point of each lateral margin. Secondary orifice inclined distally, roughly circular, with large, median mucro flanked on either side by a much smaller denticle.

Avicularia adventitious, but nearly of interzooecial position, paired, occupying large, slightly swollen chambers on lateral margins of zooecia just proximal to orifice. Rostrum pointed, attenuated, directed transversely outwards. Pivotal bar complete.

Ovicell hyperstomial, globular, elongate, opening broadly into peristome, the lip of the ovicell forming a convex projection into secondary orifice. Surface convex, irregularly perforated with numerous small pores between radiating, costule-like ridges. Orifice of fertile zooecium not modified.

MEASUREMENTS :

Lz (7) 0·552 (0·0640) mm., 0·47–0·68 mm.
lz (6) 0·398 (0·0461) mm., 0·35–0·48 mm.
ho (5) 0·123 (0·0167) mm., 0·10–0·14 mm. } secondary orifice
lo (5) 0·176 (0·0076) mm., 0·17–0·19 mm.
Lav (7) 0·184 (0·0396) mm., 0·14–0·26 mm.
Lov (2) 0·321 (0·0302) mm., 0·30–0·34 mm.

REMARKS. Balavoine (1960 : 246) included this species in his list from the Lutetian of Bois-Gouët (Loire-Atlantique) with the annotation that Canu (1908) had found it, but that it was missing from his (Balavoine's) material. At the same time he (1960 : 247) described *Romancheina gouetensis* as a new species similar to *E. aliferus* but having a uniformly perforate (" tremocystal ") frontal. His figures (1960 : pl. 6, figs. 11–14 ; pl. 7, figs. 1–4) show, however, not tremopores but areolae in the double lateral rows characteristic of the frontal of *E. aliferus* where it is joined by the avicularian chambers. Thus there is little doubt that Balavoine's species is the one correctly identified by Canu with *E. aliferus*.

The pore-chambers of the Upper Bracklesham specimens are very small and difficult to identify.

DISTRIBUTION. Eocene (Lutetian) ; France. Eocene (Ludian) ; Italy, Hungary, Poland, Rumania.

Family **SMITTINIDAE** Levinsen

Genus ***SMITTOIDEA*** Osburn

1952 *Smittoidea* Osburn : 408.

TYPE SPECIES (by original designation). *Smittoidea prolifica* Osburn 1952 : 408, pl. 48, figs. 7, 8. Recent ; Californian coast, U.S.A.

DIAGNOSIS. Frontal wall calcareous, smooth, granular, or tuberculate, with a single row of marginal areolae proximally and laterally. Orifice sub-circular to semi-circular with well-developed condyles and a median proximal lyrula. Peristome high distally and laterally, usually with a proximal notch ; spines, if present, evanescent. Avicularium adventitious, frontal, median sub-oral, placed within peristomial sinus or just proximal to it, rostrum directed longitudinally proximally. Ovicell hyperstomial, evenly and numerously perforated.

REMARKS. Before Osburn's sweeping revision of the family Smittinidae (1952 : 390–440), almost all Tertiary Smittinids were placed in either *Smittina* or *Porella*, both of which had become ungainly (see Lagaaij 1952 : 97, for a discussion of the nomenclatorial difficulties attending these genera). *Smittina*, as now restricted, includes species having an evenly perforated frontal, a median sub-oral avicularium, the orifice with lyrula and condyles, and an evenly perforated ovicell. Revision of the Eocene and Oligocene species which have in the past been assigned to *Smittina* and *Porella* will be a major undertaking. The list of species assignable to *Smittoidea* may be started with the following : *Smittia variabilis* Canu (described below) from the Eocene of England, Belgium, and France ; *Smittina angulata* (Münster) (Dartevelle 1952 : 191) from the Oligocene of Germany ; *Smittina orbavicularia* Canu & Bassler (1920: 469, pl. 61, figs. 1–4) from the Eocene of the Gulf Coast of the U.S.A. ; and *Smittina telum* Canu & Bassler (1920 : 468, pl. 93, figs. 1–9) and *Smittina reticuloides* Canu & Bassler (1920 : 467, pl. 96, figs. 1–9) from the Oligocene of the Gulf Coast, U.S.A.

Smittoidea variabilis (Canu)

(Text-figs. 42–47)

1908 *Smittia* (*Porella*) *variabilis* Canu : 97, pl. 8, figs. 1–7.
1929*a* *Smittina variabilis* (Canu) Canu & Bassler : 40.
1933 *Smittina variabilis* (Canu) ; Dartevelle : 107.
?1933 *Palmicellaria lerichei* Dartevelle : 82, pl. 3, figs. 3, 4.
1934 *Smittina variabilis* (Canu) ; Davis : 223, pl. 15, fig. 54.
1937 *Smittina variabilis* (Canu) ; Dartevelle : 110.
1946 *Smittina variabilis* (Canu) ; Buge : 435.
1949 *Porella variabilis* (Canu) Balavoine : 774.
1956 *Smittina variabilis* (Canu) ; Balavoine : 322.
1957 *Smittina variabilis* (Canu) ; Balavoine : 192.
?1963 *Trigonopora monilifera* (Milne Edwards) ; Malecki : 130, pl. 14, fig. 1 [*non Eschara monilifera* Milne Edwards].

FIGURED SPECIMENS. D.48676 (Text-fig. 42), D.48677 (Text-fig. 43), D.48678 (Text-fig. 44), D.48679 (Text-fig. 45), D.48679 (Text-figs. 46, 47).

ADDITIONAL MATERIAL. Forty-eight specimens, D.48680–D.48727.

DIAGNOSIS. Encrusting or erect, uni- or bilaminar *Smittoidea* with zooecia extremely variable in size and form depending on zoarial type ; on encrusting portions, zooecia short, with thick, smooth frontals, well-developed peristomes, and large sub-oral avicularium on protuberant umbo ; on erect portions, zooecia longer, with thinner, coarsely tuberculate frontals, short peristomes, and smaller avicularia or none ; orifice large, semi-circular, with stout condyles and a rudimentary lyrula ; oral spines lacking ; ovicell very wide and finely perforate.

Description. *Zoarium* encrusting, unilaminar, rising in uni- or bilaminar, erect fronds, the zooecia crudely aligned in longitudinal rows on unilaminar portions, regularly aligned in alternating series on bilaminar.

Zooecia on unilaminar portions irregularly hexagonal, pentagonal, or tetragonal, separated by narrow, salient threads. Length nearly one and a half times width. Frontal wall very convex and thick, highest at sub-oral umbo. Surface smooth, almost hyaline, with 3–4 large areolae in a single row on each proximo-lateral margin. Interareolar costules feebly developed, peripheral. Sub-oral umbo large, salient, massive. *Orifice* deeply buried in peristome, large, semi-circular, the distal margin evenly rounded, the proximal margin slightly convex, forming an incipient lyrula. Condyles paired, stout, placed on lateral margins close to proximal lip. Peristome irregular, forming a pair of high, lateral lappets, coalescing with the umbo, and a lower distal collar. Secondary orifice variable in shape depending on relative development of umbo, lappets, and avicularium.

Zooecia on bilaminar portions rectangular to rhomboidal, separated by narrow, raised threads. Length more than twice width. Frontal wall moderately convex and thick, highest near centre, except where avicularium is present. Surface smooth and almost hyaline at first but becoming coarsely tuberculate and porcellanous as calcification progresses. Areolae 5–7 along each proximo-lateral margin, without costules. Sub-oral umbo lacking, the avicularium, where present, occupying a swollen chamber covering most of the frontal surface. *Orifice* shallow, sub-terminal on frontal surface, large, semi-circular, the distal margin evenly rounded, the proximal margin convex, with a well-developed, broad, tapering, median lyrula. Condyles rudimentary. Peristome very short and thin, without distinct lateral lappets.

Avicularium adventitious, usually lacking on bilaminar fronds, single, median, sub-oral, placed on umbo or in swollen frontal chamber, usually facing into peristome, but with rostrum directed frontally and proximally. Rostrum rounded ; pivotal bar complete.

Ovicell hyperstomial, large, globular, wider than long, present on both uni- and bilaminar portions of zoarium. Surface evenly perforated with very small pores. Distal and lateral margins distinctly rimmed. Proximal margin obscured by elongated and inwardly bent peristomial lappets.

Measurements :

Zooecia on unilaminar portions

Lz	(10) 0·447	(0·0661) mm.,	0·31–0·56 mm.
lz	(10) 0·325	(0·0397) mm.,	0·23–0·36 mm.
ho	(10) 0·120	(0·0121) mm.,	0·10–0·14 mm.
lo	(10) 0·146	(0·0130) mm.,	0·13–0·17 mm.
Lav	(5) 0·109	(0·0185) mm.,	0·09–0·13 mm.
Lov	(3) 0·239	(0·0171) mm.,	0·22–0·26 mm.

Zooecia on bilaminar portions

Lz (10) 0·634 (0·1055) mm., 0·48–0·88 mm.
lz (10) 0·288 (0·0586) mm., 0·25–0·44 mm.
ho (10) 0·122 (0·0110) mm., 0·09–0·13 mm.
lo (10) 0·143 (0·0107) mm., 0·13–0·16 mm.
Lav (2) 0·111 (0·0121) mm., 0·10–0·12 mm.
Lov (4) 0·177 (0·0146) mm., 0·16–0·20 mm.

REMARKS. There is so much difference in the appearance of the zooecia on the uni- and bilaminar fragments that they might easily be mistaken for distinct species. As in the Lower Bracklesham Beds (Davis 1934 : 223), unilaminar fragments account for the majority of Upper Bracklesham specimens.

Although the illustrations of *Palmicellaria lerichei* Dartevelle (1933 : pl. 3, figs. 3, 4) are not completely clear, they resemble the general aspect of bilaminar fragments of *S. variabilis*.

The bilaminar fragment described and illustrated by Malecki (1963 : 130, pl. 14, fig. 1) as *Trigonopora monilifera* is almost certainly referable to *S. variabilis*. The globular hyperstomial ovicell (described as entozooecial), the deeply notched peristome, and the median sub-oral avicularium are evident on the figure. Specimens from the Eocene of Rumania (supplied by Dr. Sten Schager) are identifiable with this species and similar to the one illustrated by Malecki.

DISTRIBUTION. Eocene (Lutetian) ; England, Belgium, France. Eocene (Auversian) ; Belgium. Eocene (Ludian) ; Rumania, ?Poland.

Family **ESCHARELLIDAE** Levinsen

Genus ***ESCHARELLA*** Gray

Escharella selseyensis sp. nov.

(Text-figs. 48–50)

1908 *Smittia* (*Mucronella*) *hoernesi* (Reuss) ; Canu : 96, pl. 7, fig. 16.
1946 *Mucronella angustoecium* Gregory ; Buge : 435.

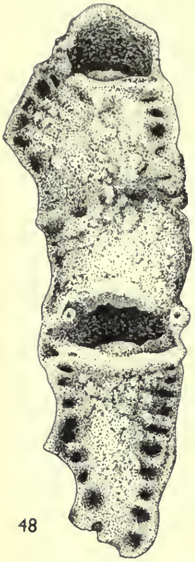
HOLOTYPE. D.48728 (Text-fig. 48).

PARATYPES. D.48729 (Text-figs. 49, 50), D.48730, and L.S.U. 8035.

DIAGNOSIS. Unilaminar, probably encrusting *Escharella* with broad lyrula in primary orifice and peristome raised proximally to form a broad, lip-like mucro ; distal margin of orifice with 2 small, evanescent spines ; ovicell large, globular.

DESCRIPTION. *Zoarium* unilaminar, presumably encrusting, with zooecia arranged in regular longitudinal rows, those in adjacent rows alternating in position.

Zooecia elongate oval, more broadly rounded distally than proximally, separated by a narrow, raised thread. Length nearly twice width. Frontal wall moderately thick, strongly convex, highest near centre. Frontal surface coarsely granular, sometimes with a large, protruding umbo covering the greater part. Areolae large,



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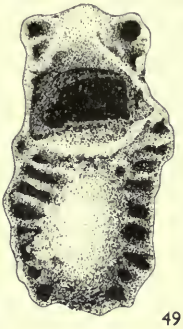

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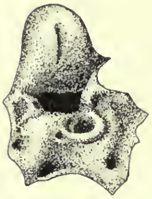

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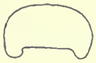

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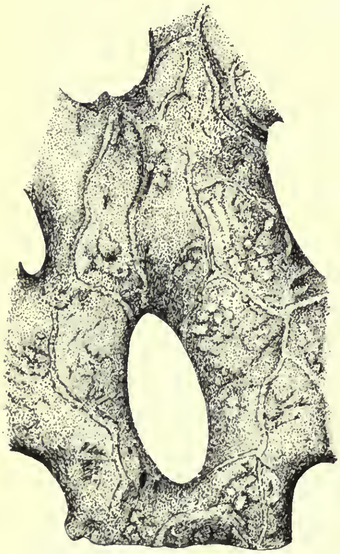

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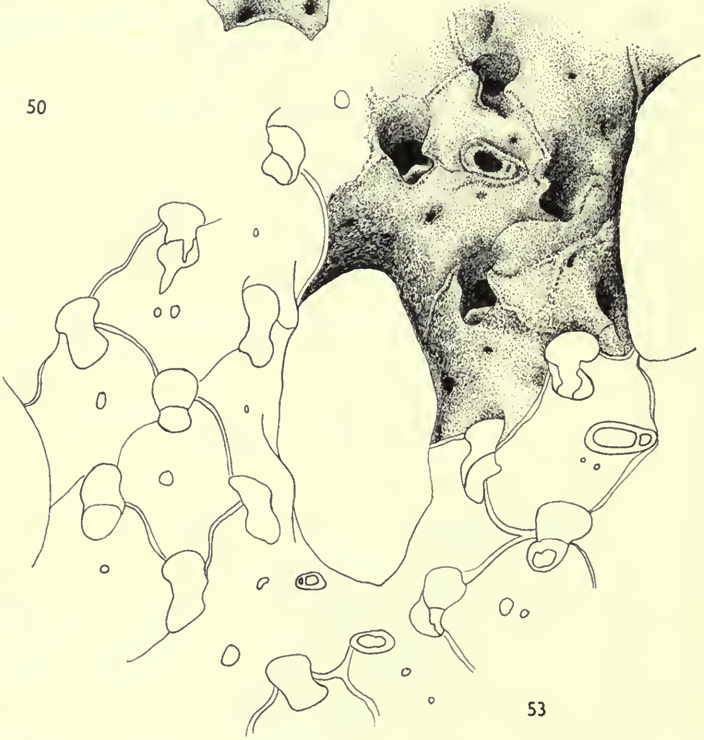

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elliptical, in a single, evenly spaced row of 16–20 on lateral and proximal margins. Inter-areolar costules short, thin, peripheral.

Orifice steeply inclined distally, deeply buried in peristome, semi-elliptical, with long axis transverse, the distal margin broadly rounded, the proximal margin straight or convex, with a broad, saddle-shaped, median lyrula. Peristome thin, granular, especially raised proximally to form a broad, lip-like mucro. Secondary orifice elliptical, with major axis transverse. Distal spines 2, small, evanescent.

Ovicell hyperstomial, globular; distal margin evenly rounded, marked by an irregular row of small areolae; proximal margin with a slightly thickened, arcuate rim. Surface coarsely granular, impunctate.

Heterozooecia lacking.

MEASUREMENTS:

Lz (8) 0·491 (0·0754) mm., 0·35–0·59 mm.
lz (5) 0·274 (0·0337) mm., 0·22–0·31 mm.
ho (6) 0·081 (0·0105) mm., 0·07–0·09 mm.
lo (5) 0·152 (0·0072) mm., 0·14–0·16 mm.
Lov (5) 0·219 (0·0130) mm., 0·20–0·24 mm.

REMARKS. The synonymy given by Canu (1908 : 96; 1913 : 149) for *Lepralia hoernesi* Reuss was considered to be heterogeneous by Canu & Bassler (1929*a* : 45). Canu's (1914*b*) Stampian material is probably conspecific with Reuss's (1865) Oligocene specimens, and both are probably referable to *Perigastrella*. Canu's (1908) Lutetian material is identifiable with the Upper Bracklesham specimens for which the name *Escharella selseyensis* is here proposed. *Mucronella angustoecium* Gregory, the Bartonian species (holotype, 49739, Edwards Collection, Barton, Hants) placed in synonymy by Canu (1908 : 96), differs from *E. selseyensis* in having larger zooecia with smaller, sub-circular orifices, and smaller ovicells.

DISTRIBUTION. Eocene (Lutetian); France.

Family **SERTELLIDAE** Jullien

Genus ***SERTELLA*** Jullien

Sertella marginata (Reuss)

(Text-figs. 51–53)

1865 *Retepora marginata* Reuss : 661, pl. 10, figs. 6, 7.
?1866 *Retepora marginata* Reuss; Reuss : 190.

FIGS. 48–53. Fig. 48. *Escharella selseyensis* sp. nov. D.48728. Holotype. Two zooecia, the proximal one ovicelled. Figs. 49, 50. *Escharella selseyensis* sp. nov. D.48729. Paratype. Zooecium with well-developed frontal umbo, and oral outline of another zooecium. Fig. 51. *Sertella marginata* (Reuss). D.48731. Dorsal aspect of a fragmentary zoarium. An avicularium occurs just over the fenestrule. Fig. 52. *Sertella marginata* (Reuss). D.48732. Ovicelled zooecium. Fig. 53. *Sertella marginata* (Reuss). D.48733. Part of a zoarial fragment showing zooecia with oral and frontal avicularia and several with fenestral ones as well.

FIGURED SPECIMENS. D.48731 (Text-fig. 51), D.48732 (Text-fig. 52), D.48733 (Text-fig. 53).

ADDITIONAL MATERIAL. Six specimens, D.48734–D.48739.

DIAGNOSIS. *Sertella* with triserial trabeculae of about same width as the elliptical fenestrules; zooecia frontally marginate with non-denticulate primary orifice and sinuate secondary orifice; oral avicularium mucronate; frontal avicularia rounded; fenestral avicularium pointed; dorsal avicularia spatulate.

DESCRIPTION. *Zoarium* erect, unilaminar, reticulated, the fenestrules elliptical, quincuncially arranged, of about same width as branches. Zooecia disposed in 3 longitudinal rows on frontal face of branch (trabecula), those in adjacent rows alternating in position. Dorsal face finely tuberculate, divided into large, irregular polygons by narrow, slightly raised threads (vibices).

Zooecia irregularly polygonal, separated by thick, low threads connecting orifices of adjoining rows. Zooecial length about one and a half times width. Frontal wall very thick, slightly convex. Surface smooth, imperforate.

Orifice deeply buried in peristome, not visible in frontal aspect, small, elliptical, with long axis transverse and proximal lip straight. No condyles or denticles present. Peristome very long but almost completely immersed in thick frontal wall. Secondary orifice pyriform, with wide, deep proximal notch. A small, evanescent spine base occurs at mid-length on each lateral margin.

Avicularia adventitious, frontal and dorsal, usually multiple and polymorphic: (1) *Oral*, single, of intermediate size, placed in proximal notch of secondary orifice, the rounded, non-mucronate rostrum projecting frontally; cross-bar complete. (2) *Ordinary-frontal*, single or paired, very small, placed on frontal wall, removed from orifice, rounded, without pivotal structure. (3) *Fenestral-frontal*, single, large, placed on frontal wall of zooecia in neighbourhood of fenestrules, the pointed rostrum directed transversely outwards; cross-bar complete. (4) *Dorsal*, large, widely scattered, the spatulate rostrum oriented more or less transversely to the axis of the trabecula; cross-bar complete.

Ovicell hyperstomial, elongate, globular, but flattened proximally. Surface smooth, with longitudinal fissure extending nearly whole length, narrow, often fusiform, the greatest width at mid-length or slightly distal to it.

MEASUREMENTS:

Length of fenestrule (6) 0·640 (0·1170) mm., 0·51–0·82 mm.
Width of fenestrule (6) 0·294 (0·0655) mm., 0·23–0·42 mm.
Lz (10) 0·307 (0·0195) mm., 0·27–0·32 mm.
lz (4) 0·175 (0·0110) mm., 0·16–0·19 mm.
ho (5) 0·056 (0·0098) mm., 0·04–0·07 mm. } secondary orifice
lo (6) 0·054 (0·0070) mm., 0·04–0·06 mm. }
Lov (6) 0·155 (0·0137) mm., 0·14–0·17 mm.
Lav (oral) (5) 0·051 (0·0105) mm., 0·04–0·07 mm.
Lav (frontal) (4) 0·030 (0·0049) mm., 0·02–0·03 mm.

Lav (fenestral) (3) 0·111 (0·0086) mm., 0·10–0·12 mm.
Lav (dorsal) (2) 0·115 (0·0181) mm., 0·10–0·13 mm.

REMARKS. This species is very much like the type species of *Sertella, S. beaniana* (King), from which it differs primarily in having trabeculae and fenestrules of about the same width, secondary orifice with sinus, fenestral avicularia pointed rather than spatulate, and dorsal avicularia large and spatulate. Although Reuss's figures (1865, pl. 10, figs. 6, 7) are not completely clear, the Upper Bracklesham specimens seem to agree with them.

DISTRIBUTION. Oligocene (Stampian) ; Germany. ?Miocene ; Germany.

Family **SCHIZOPORELLIDAE** Jullien

Genus ***DAKARIA*** Jullien

1903 *Dakaria* Jullien *in* Jullien & Calvet : 90.

TYPE SPECIES (by original designation). *Dakaria chevreuxi* Jullien *in* Jullien & Calvet 1903 : 90, pl. 10, fig. 6. Recent ; off Dakar, Senegal.

DIAGNOSIS. Frontal wall calcareous, evenly perforated with numerous pores. Orifice with broad, rounded, proximal sinus. Avicularia lacking. Ovicells, if present, hidden from frontal view.

REMARKS. This deceptively simple Schizoporellid genus is not yet completely understood. Harmer's (1957 : 1021) inclusion of *Watersipora* and *Cribella* in its synonymy is open to question.

Dakaria beyrichi (Stoliczka)

(Text-fig. 54)

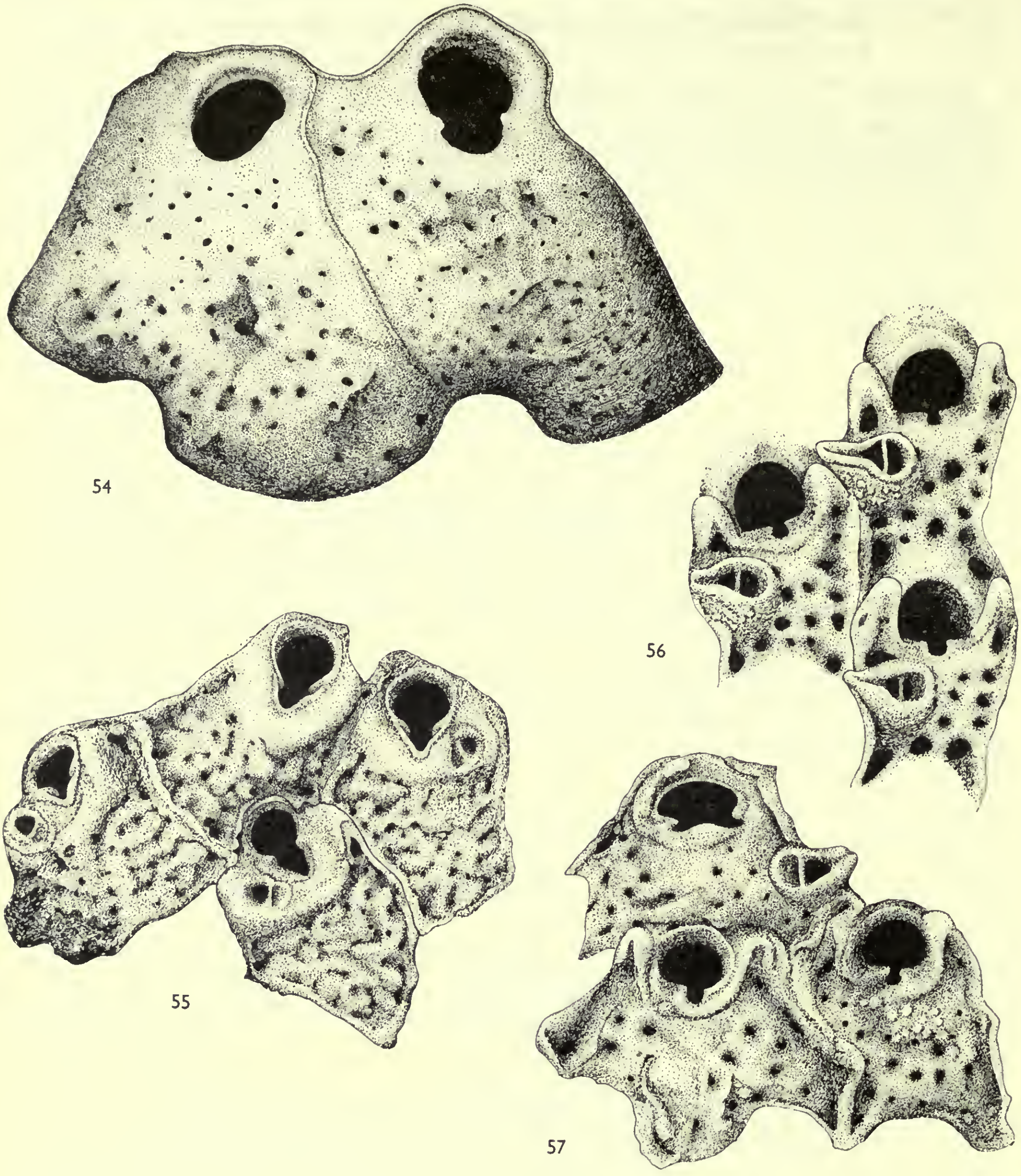
1862 *Cellaria beyrichi* Stoliczka : 83, pl. 1, fig. 10.
1908 *Hippoporina beyrichi* (Stoliczka) Canu : 83, pl. 6, fig. 2.
1935 *Dakaria beyrichi* (Stoliczka) Dartevelle : 115.
1946 *Hippoporina beyrichi* (Stoliczka) ; Buge : 434.
1952 *Dakaria beyrichi* (Stoliczka) ; Dartevelle : 190.
1956 *Dakaria beyrichi* (Stoliczka) ; Balavoine : 322.

FIGURED SPECIMEN. D.48740 (Text-fig. 54).

DIAGNOSIS. Erect, cylindrical *Dakaria* with large, simple orifice lacking a peristome ; ovicell unknown.

DESCRIPTION. *Zoarium* erect, cylindrical, the zooecia in 6–8 alternating, longitudinal rows.

Zooecia irregularly rhombic, separated by a faint groove at the crest of a wide, low thread. Zooecial length slightly less than width. Frontal wall moderately thick, very convex, highest near centre. Surface smooth, evenly perforated with numerous, small, circular, quincuncially arranged pores.



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Figs. 54–57. Fig. 54. *Dakari beyrichi* (Stoliczka). D.48740. Two zooecia. Fig. 55. *Schizomavella trigonostoma* sp. nov. D.48741. Holotype. Four zooecia, the one at upper left without an avicularium. Fig. 56. *Escharina procumbens* (Canu). D.48742. Three ovicelled zooecia from a unilaminar zoarial fragment. Fig. 57. *Escharina procumbens* (Canu). D.48743. Three non-ovicelled zooecia from a bilaminar fragment. The upper zooecium has the right margin of its orifice broken.

Orifice terminal on frontal surface, slightly inclined distally, the distal half slightly more than a semi-circle, the proximal sinus a slightly smaller semi-circle. Peristome, condyles lacking.

Heterozooecia lacking.

Ovicell unknown.

MEASUREMENTS :

Lz (4) 0·635 (0·0409) mm., 0·59–0·68 mm.
lz (4) 0·667 (0·0908) mm., 0·56–0·77 mm.
ho (5) 0·180 (0·0337) mm., 0·13–0·22 mm.
lo (5) 0·161 (0·0112) mm., 0·14–0·17 mm.

DISTRIBUTION. Eocene (Ypresian, Lutetian) ; France. Eocene (Lutetian) ; Belgium. Oligocene (Lattorfian) ; Germany.

Genus ***SCHIZOMAVELLA*** Canu & Bassler

?1893 *Schismoporella* Gregory : 243.
1917 *Schizomavella* Canu & Bassler : 40.
1917 *Metroperiella* Canu & Bassler : 40.

TYPE SPECIES (by original designation). *Lepralia auriculata* Hassall 1842 : 411. Recent ; British Isles.

DIAGNOSIS. Frontal wall calcareous, evenly perforated with numerous pores. Orifice oval, with distinct median-proximal sinus between small condyles; sinus usually rounded and shallow. Peristome low, usually thin. Avicularium adventitious, single, frontal, proximal to orifice, directed longitudinally proximally or transversely, sometimes placed on a sub-oral umbo. Ovicell hyperstomial, globular, perforate.

REMARKS. Harmer (1957 : 1024–1027) considered *Metroperiella* a distinct genus by virtue of its large ovicell surrounding the orifice of the ovicelled zooecium, but fossil species are intermediate between the two extremes. Buge (1953 : 322) regarded *Schismoporella* as a genus distinguishable from *Schizomavella* in having the avicularium removed from the orifice. Unfortunately, no such regularity of position as Buge implied characterizes these Schizoporellids (see e.g., Canu & Bassler 1920 : pl. 46, figs. 4–17 ; Brown 1952 : 235–238). Moreover, the type species of *Schismoporella, Lepralia schizogaster* Reuss (1848 : 84, pl. 10, fig. 9), requires re-study before its generic affinities can be definitely established. If it proves to be congeneric with *Schizomavella auriculata*, then *Schismoporella* will, of course, be the correct name of the genus.

Schizomavella trigonostoma sp. nov.

(Text-fig. 55)

HOLOTYPE. D.48741 (Text-fig. 55).

PARATYPE. L.S.U. 8036.

Diagnosis. Erect, bilaminar *Schizomavella* with rounded-trigonal orifice, the large, V-shaped sinus limited by stout lateral condyles; avicularium placed on proximo-lateral margin of orifice, the rostrum directed obliquely distally and outwards.

Description. *Zoarium* erect, bilaminar, compressed or cylindrical, the zooecia arranged in irregular longitudinal rows, those in adjacent rows alternating in position.

Zooecia irregularly rhomboidal, separated by a narrow, salient thread. Zooecial length slightly greater than width. Frontal wall moderately thick, slightly convex, highest near centre. Surface granular, evenly perforated with numerous, small, circular, quincuncially arranged pores.

Orifice entirely visible in frontal view, small, terminal on frontal wall, rounded trigonal, the distal margin evenly rounded, the proximal portion consisting of a very large, V-shaped sinus limited on each side by a stout, proximally directed condyle. Peristome thick but very low, widest proximally, smooth, flaring outwards.

Avicularium adventitious, single, frontal, placed on proximo-lateral margin of orifice, partly buried in peristome, with rostrum directed obliquely distally and outwards. Rostrum rounded. Pivotal bar complete.

Ovicell unknown.

Measurements:

Lz (5) 0·477 (0·0584) mm., 0·38–0·52 mm.
lz (5) 0·397 (0·1013) mm., 0·33–0·57 mm.
ho (6) 0·137 (0·0171) mm., 0·12–0·16 mm.
lo (6) 0·107 (0·0054) mm., 0·10–0·11 mm.
Lav (5) 0·128 (0·0191) mm., 0·10–0·15 mm.

Remarks. The orifice of this species, with a much longer sinus and stronger condyles than are typical of *Schizomavella*, finds a parallel in *S. dubia* Brown (1952 : 235, text-figs. 168, 169) from the Pliocene of New Zealand. The avicularium of *S. trigonostoma*, also atypical of *Schizomavella*, is similar in form, position, and orientation to that of *S. australis* (Haswell) (see Harmer 1957 : 1031, pl. 66, fig. 9).

Genus *ESCHARINA* Milne Edwards

Escharina procumbens (Canu)

(Text-figs. 56, 57)

1910 *Schizoporella hoernesi* var. *procumbens* Canu : 853, pl. 19, fig. 5.
1916 *Schizoporella hoernesi* (Reuss) ; Faura y Sans & Canu : 298.
1950 *Schizoporella hoernesi* (Reuss) ; Barroso : 179, text-fig. 7.

Figured specimens. D.48742 (Text-fig. 56), D.48743 (Text-fig. 57).

DIAGNOSIS. Unilaminar or bilaminar, probably erect *Escharina* with somewhat elongate zooecia having coarsely perforate frontal and comparatively large orifice ; avicularium large, single, transversely and outwardly directed, with raised, swollen chamber ; a grooved, protuberant boss is developed from a frontal pore on each side of the orifice.

DESCRIPTION. *Zoarium* unilaminar, probably erect, tubular, sometimes becoming bilaminar, with zooecia arranged in longitudinal rows, those in adjacent rows alternating in position.

Zooecia irregularly rectangular to rhomboidal, separated by a narrow, raised thread. Length nearly one and a half times width. Frontal wall very slightly convex, moderately thick. Frontal surface finely tuberculate, perforated with large, evenly spaced pores, those along the margins tending to be larger.

Orifice large, semi-circular, completely visible in frontal view. Distal margin evenly rounded ; proximal margin nearly straight, interrupted medially by a narrow, shallow, rounded sinus. Peristome rudimentary. On each side of orifice occurs a tall, proximally grooved, protuberant boss originating from a frontal pore.

Avicularium adventitious, single or absent, large, frontal, placed on lateral margin at about mid-length, its rostrum transversely outwardly directed. Chamber slightly raised and swollen, the exterior tuberculate but imperforate. Rostrum channelled, pointed, produced slightly beyond border of zooecium. Pivotal bar complete.

Ovicell hyperstomial, recumbent, deeply immersed in distal zooecium, forming a small, hood-like swelling at distal margin of orifice. Surface imperforate, finely tuberculate, the proximal margin thickened, the distal margin merging with frontal wall of distal zooecium.

MEASUREMENTS :

Lz (7) 0·385 (0·0401) mm., 0·32–0·43 mm.
lz (7) 0·291 (0·0651) mm., 0·23–0·38 mm.
ho (7) 0·127 (0·0104) mm., 0·11–0·14 mm.
lo (8) 0·123 (0·0111) mm., 0·10–0·11 mm.
Lav (3) 0·154 (0·0171) mm., 0·14–0·17 mm.
Lov (2) 0·171 (0·0000) mm., 0·17 mm.

REMARKS. The Upper Bracklesham specimens agree best with the material from the Bartonian of Spain illustrated by Barroso (1950, text-fig. 7), from which they differ only in having well-developed lateral-oral bosses. The French specimens figured by Canu (1910 : pl. 19, fig. 5) have more numerous, smaller frontal pores and less-developed bosses. *E. hoernesi* (Reuss) has much more slender zooecia, smaller frontal pores, and much smaller avicularia in addition to lacking oral bosses entirely. Ovicells have not been noted heretofore in *E. procumbens*, though Reuss (1869*a* : pl. 33, figs. 6, 7) illustrated similar ones in *E. hoernesi*.

DISTRIBUTION. Eocene (Lutetian, ?Auversian) ; France. Eocene (Lutetian, Bartonian) ; Spain.

Family **HIPPOPODINIDAE** Levinsen

Genus ***HIPPOPORINA*** Neviani

Hippoporina globulosa (d'Orbigny)

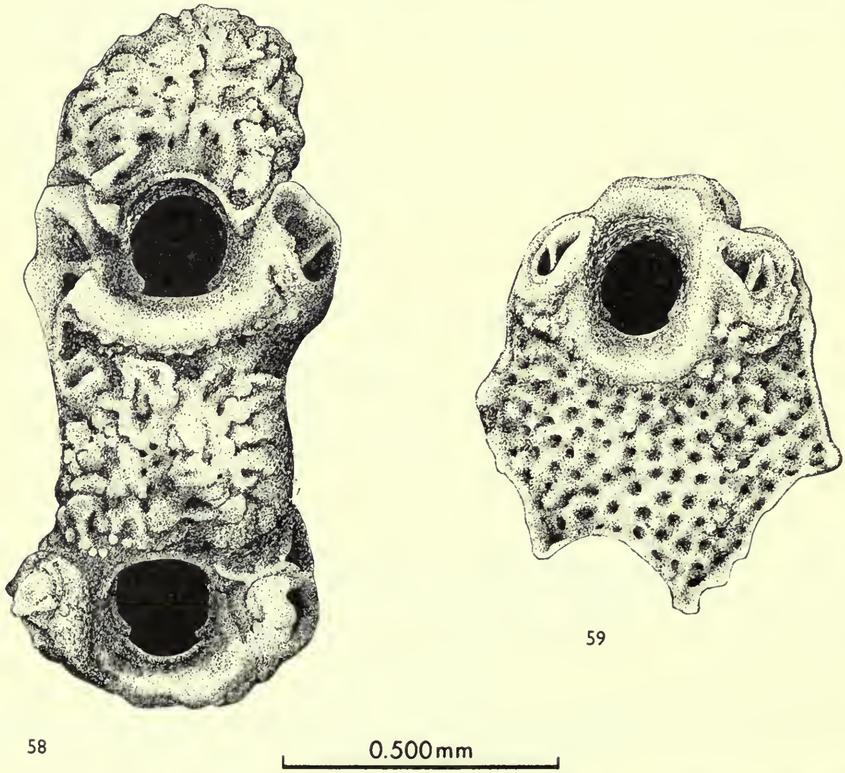
(Text-figs. 58, 59)

1851 *Reptescharellina globulosa* d'Orbigny : 453.
1908 *Hippoporina globulosa* (d'Orbigny) ; Canu : 82, pl. 6, fig. 9.
1933 *Hippoporina globulosa* (d'Orbigny) ; Dartevelle : 77.
1946 *Hippoporina globulosa* (d'Orbigny) ; Buge : 434.

FIGURED SPECIMENS. D.48744 (Text-fig. 58), D.48745 (Text-fig. 59).

DIAGNOSIS. Nodular, encrusting *Hippoporina* with paired, lateral-oral avicularia, the rostra directed inwards and distally ; ovicell large, globular, evenly perforated ; oral condyles stout, very close to proximal lip.

DESCRIPTION. *Zoarium* unilaminar, encrusting, forming irregularly globular masses, with the zooecia arranged in longitudinal rows, those in adjacent rows alternating in position.



FIGS. 58–59. Fig. 58. *Hippoporina globulosa* (d'Orbigny). D.48744. Two ovicelled zooecia, the proximal one incomplete. Fig. 59. *Hippoporina globulosa* (d'Orbigny). D.48745. Ordinary zooecium.

Zooecia irregularly rectangular, pentagonal, or rhomboidal, rounded distally, separated by narrow, sharp, raised threads. Zooecial length slightly greater than width. Frontal wall moderately thick, slightly convex, highest at proximal margin of peristome. Surface evenly perforated with numerous, closely spaced, quincuncially arranged, circular, funnel-shaped pores. Surface between pores ridged in a reticulate pattern, the intersections of the ridges often marked by small tubercles.

Orifice entirely visible in frontal view, large, elliptical, with major axis longitudinal, sub-terminal, slightly inclined distally. Condyles stout, paired, directed slightly proximally, placed on lateral margins very near proximal lip. Peristome thick but low, smooth, flaring outwards all round orifice, enclosing a very narrow, crescent-shaped bare spot proximally and occasionally distally as well.

Avicularia adventitious, frontal, paired, placed on lateral margins of peristome with rostra directed inwards and distally on to peristome. Rostrum pointed but not produced. Pivotal bar complete.

Ovicell hyperstomial, large, globular, deeply sunk in distal zooecium, but with proximal margin arching above orifice of ovicelled zooecium. Surface evenly perforated with numerous pores like those on frontal wall. Distal and proximal margins without rims. Orifice of ovicelled zooecia unmodified.

Measurements :

Lz (4) 0·646 (0·1037) mm., 0·56–0·77 mm.
lz (4) 0·517 (0·0649) mm., 0·45–0·61 mm.
ho (4) 0·156 (0·0108) mm., 0·14–0·17 mm.
lo (4) 0·162 (0·0070) mm., 0·15–0·17 mm.
Lav (3) 0·177 (0·0049) mm., 0·17–0·18 mm.
Lov (3) 0·399 (0·0131) mm., 0·38–0·41 mm.

Remarks. D'Orbigny (1851) did not illustrate his material; the holotype (Muséum national d'Histoire naturelle, Paris, no. 9648) was figured by Canu (1908 : pl. 6, fig. 9).

Distribution. Eocene (Lutetian, Auversian) ; France. Eocene (Auversian) ; Belgium.

Family **DITAXIPORINIDAE** Cheetham

Genus ***CABEROIDES*** Canu

1908 *Caberoides* Canu : 87.

Type species (by original designation). *Caberoides canaliculatus* Canu 1908 : 88, pl. 11, figs. 11, 12. Eocene (Lutetian) ; vicinity of Paris, France.

Diagnosis. Frontal wall calcareous, convex, irregularly perforated with scattered pores of variable size. Orifice terminal on frontal surface, broadly sinuate between small, widely spaced condyles proximally. Peristome thin, short. Interzooecial communication by simple pores. Vibracula adventitious, paired, with elongate chambers on frontal surface ; additional oblique, slit-like vibracula sometimes present on dorsal surface, following interzooecial sutures. Avicularium single, adventitious, placed on outer margin of zooecium, either above or below vibraculum, with short, pointed rostrum directed distally and outwards. Ovicell hyperstomial, elongate, globular, curved outwards from zooecial mid-line, ornamented with irregularly placed pores. Zoarium erect, jointed, branching at internodes ; internodes biserial, with orifices opening on one face only.

REMARKS. Canu (1908 : 87) introduced this genus for two French Lutetian species, *C. canaliculatus*, the type, and *C. grignonensis* Canu (1908 : 88, pl. 11, figs. 14, 15), both of which display dorsal vibracula in addition to the frontal ones and have the frontal avicularium placed above the outer vibraculum. *C. corniculatus* sp. nov., described below, lacks dorsal vibracula and has the avicularium below the outer vibraculum.

The genus *Caberoides*, constituted of these three species, ranges from Lutetian to Auversian and is endemic to the Anglo–Paris Basin. I have earlier (Cheetham 1963*a* : 489) remarked upon the similarity of *Caberoides* and *Ditaxiporina* Stach and at that time erected the family Ditaxiporinidae for them.

Caberoides corniculatus sp. nov.

(Text-figs. 60, 61)

HOLOTYPE. D.48746 (Text-figs. 60, 61).

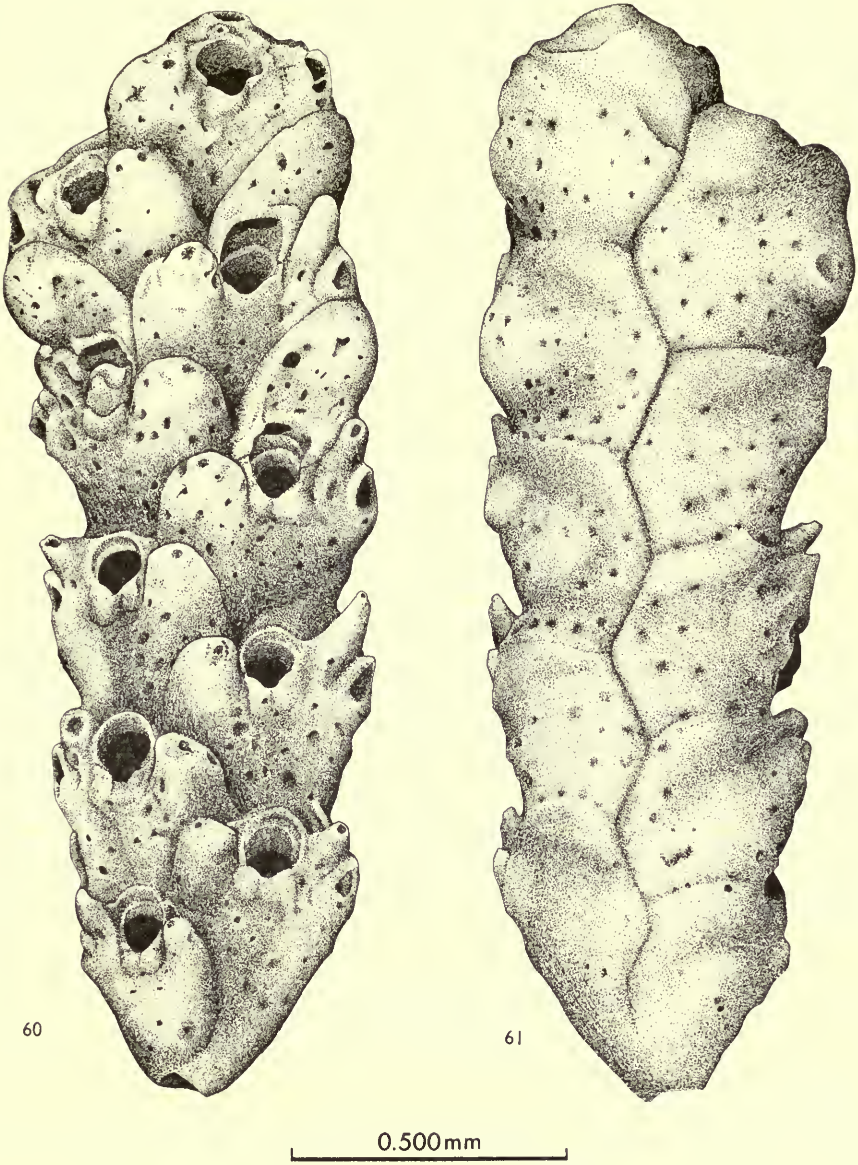
PARATYPES. D.48747–D.48771 (25 specimens), and L.S.U. 8037.

DIAGNOSIS. *Caberoides* with vibracula on frontal side only, paired, the outer one elongate and horn-like ; avicularium placed on chamber of outer vibraculum and below its opening ; ovicell curved outwards markedly, its surface with numerous, irregular perforations and 2–3 larger fenestrae.

DESCRIPTION. *Zoarium* erect, jointed, dichotomous at nodes. Internodes long, narrow, compressed, consisting of 10 or 12 zooecia arranged in 2 alternating series, with orifices all opening on one face. Proximal end of internode with single, simple, circular opening formed jointly by proximal ends of first zooecia of both series, one of which, either right or left, is slightly lower. Distal end of internode with 2 pores, one on mid-line of distal wall of last zooecium of each series.

Zooecia rhomboidal, distorted on frontal side by vibracular chambers, separated on both frontal and dorsal sides by grooves. Communication between zooecia of the same series by a single, median pore in distal wall ; between zooecia of adjacent series by simple pores along mid-line of inner lateral wall. Zooecial length slightly greater than width. Frontal wall thin, irregularly convex, highest at proximal lip of orifice. Frontal surface smooth, perforated irregularly by pores sometimes forming short tubules. Basal surface gently convex, perforated in same way as frontal.

Orifice terminal on frontal surface, large, inclined distally. Distal margin broadly and evenly rounded ; proximal margin broadly sinuate between a pair of small, widely spaced condyles. Peristome thin, short.



Figs. 60, 61. *Caberoides corniculatus* sp. nov. D.48746. Holotype. Frontal and dorsal views of a nearly complete internode, showing 10 zooecia of which three are ovicelled.

Vibracula adventitious, paired, placed on lateral margins of frontal wall, opening beside orifice. Inner vibraculum with large, bulbous chamber, perforated like frontal wall on which it reposes, extending from proximal border of zooecium to orifice; distal margin of vibraculum with crescent-shaped slit. Inner vibracula of adjacent series form an irregular, zig-zag ridge down mid-line of internode face. Outer vibraculum with long, horn-like chamber projecting outwards from lateral margin of zooecium; vibracular slit straight, running down outer margin of chamber.

Avicularium adventitious, single, small, placed on chamber of outer vibraculum below its opening. Rostrum short, pointed, directed distally and slightly outwards. Opening divided by pivotal bar at least in some specimens.

Ovicell hyperstomial, elongate, globular, curved markedly outwards from longitudinal axis of zooecium, separated from distal zooecium by a furrow. Surface convex, smooth, perforated by irregularly spaced pores, 2–3 of which are commonly larger. Opening arched but very low, probably not closed by operculum, marked by a distinct ridge.

MEASUREMENTS:

Lz (10) 0·349 (0·0224) mm., 0·32–0·37 mm.
lz (10) 0·321 (0·0340) mm., 0·26–0·37 mm.
ho (10) 0·091 (0·0092) mm., 0·08–0·10 mm.
lo (10) 0·098 (0·0073) mm., 0·09–0·10 mm.
Lav (10) 0·093 (0·0063) mm., 0·09–0·10 mm.
Lov (4) 0·297 (0·0043) mm., 0·29–0·30 mm.

REMARKS. This species differs from both *C. canaliculatus* and *C. grignonensis*, not only in the position of the frontal avicularium and in lacking dorsal vibracula, but also in its more robust zooecia. Specimens of *C. canaliculatus* from the Sables de Fresville (Lutetian) at Gourbesville (Manche), France (supplied by Mr. Dennis Curry), are shorter (mean Lz = 0·30 mm. for 5 zooecia), and specimens of *C. grignonensis* from the same sample are narrower (mean lz = 0·26 mm. for 5 zooecia). The ovicells of the Gourbesville specimens do not show the characteristic ornamentation of the ovicell described by Canu (1908: 88, 89), i.e. channelled in *C. canaliculatus* and carinate in *C. grignonensis*.

Family **TUBUCELLARIIDAE** Busk

Genus ***TUBUCELLA*** Canu & Bassler

1917 *Tubucella* Canu & Bassler: 62.

TYPE SPECIES (by original designation). *Eschara mamillaris* Milne Edwards 1836: 336, pl. 11, fig. 10. Eocene (Lutetian); vicinity of Paris, France.

DIAGNOSIS. Frontal wall calcareous, inflated, perforated with evenly spaced, quincuncially arranged pores. Orifice small, semi-circular, hidden completely by a tubular peristome equal in length to the frontal wall. Ascopore not much larger than frontal pores, simple, single, placed on frontal wall near peristomial suture.

Scattered frontal avicularia present in some species. Ovicell peristomial, a small swelling near base of peristome of fertile zooecium ; fertile peristomes of different form from infertile ones. Zoarium erect, bilaminar, not jointed.

REMARKS. This genus was established as a sub-genus of *Tubucellaria* d'Orbigny, but there is no tendency for the zoarium of *Tubucella* to be jointed, and avicularia, unknown in *Tubucellaria*, are present in many, though not the type, species of *Tubucella*.

Tubucella mamillaris (Milne Edwards)

(Text-figs. 62–64)

1836 *Eschara mamillaris* Milne Edwards : 336, pl. 11, fig. 10.
1907*a* *Tubucellaria mamillaris* (Milne Edwards) Canu : 515.
1908 *Tubucellaria mamillaris* (Milne Edwards) ; Canu : 78, pl. 6, figs. 3–6.
1910 *Tubucellaria mamillaris* (Milne Edwards) ; Canu : 848.
1917 *Tubucellaria* (*Tubucella*) *mamillaris* (Milne Edwards) ; Canu & Bassler : 62.
1918*a* *Tubucella mamillaris* (Milne Edwards) Canu : 358.
1925 *Tubucellaria mamillaris* (Milne Edwards) ; Canu : 47.
1929*a* *Tubucella mamillaris* (Milne Edwards) ; Canu & Bassler : 46.
1933 *Tubucellaria mamillaris* (Milne Edwards) ; Dartevelle : 102.
1935 *Tubucellaria mamillaris* (Milne Edwards) ; Dartevelle : 116.
1946 *Tubucellaria mamillaris* (Milne Edwards) ; Buge : 436.
1949 *Tubucella mamillaris* (Milne Edwards) ; Balavoine : 774.
1956 *Tubucella mamillaris* (Milne Edwards) ; Balavoine : 324.
1957 *Tubucella mamillaris* (Milne Edwards) ; Balavoine : 192.
1960 *Tubucella mamillaris* (Milne Edwards) ; Balavoine : 246.

FIGURED SPECIMENS. D.48772 (Text-fig. 62), D.48773 (Text-fig. 63), D.48774 (Text-fig. 64).

ADDITIONAL MATERIAL. Six specimens, D.48775–D.48780.

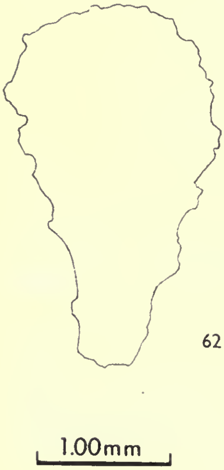
DIAGNOSIS. *Tubucella* with most of the peristome pitted, sessile, and bordered by large pores, and with the free portion longitudinally costate ; ascopore on a small frontal prominence separated from peristome by a single row of pores ; fertile perstomes short, with a disto-lateral crown of pores ; avicularia lacking.

DESCRIPTION. *Zoarium* erect, bilaminar, cylindrical to compressed, typically forming lobate or flabellate branches originating as a cylinder of 6–8 rows of zooecia and widening into flattened fronds with 12–15 rows of zooecia on each side. Zooecia arranged in longitudinal rows, those in adjacent rows alternating in position.

Zooecia elongate, tubular, consisting of two regions of about equal length : a proximal frontal region bearing the ascopore, and a distal peristome bearing the secondary orifice. Zooecia separated by narrow, low threads. Frontal wall moderately thick, slightly convex, usually somewhat elevated immediately round the ascopore. Surface evenly perforated with large, circular, quincuncially arranged pores. Ascopore slightly larger than frontal pores, tilted distally, placed very near peristomial suture, with only a single row of frontal pores between.

Orifice small, semi-circular, with straight proximal lip, tilted distally, completely hidden from frontal view by peristome. Peristome sessile for most of its length, becoming free only at distal extremity. Sessile portion pitted and bordered on each side by a row of 5–8 circular pores, larger than the frontal pores. Free portion longitudinally costate or with longitudinal rows of small tubercles. Secondary orifice circular.

Ovicell small, peristomial, formed as a globular swelling in distal wall of peristome, near its base, hidden completely from frontal view. Ovicelled zooecia with frontal wall like that of non-ovicelled ones, but with much shorter and wider sessile peristome



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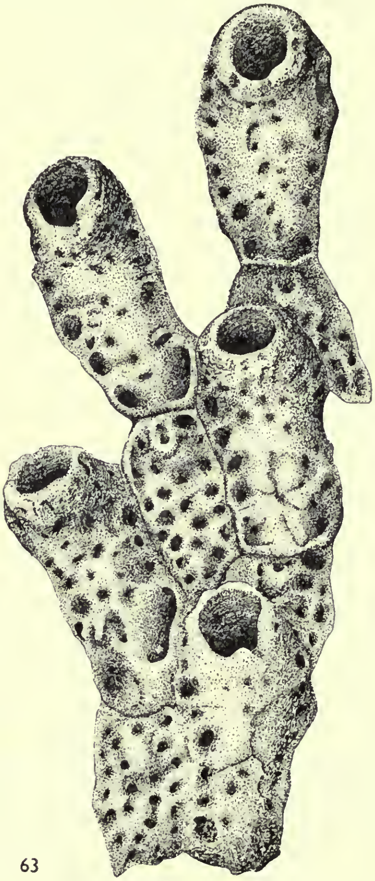

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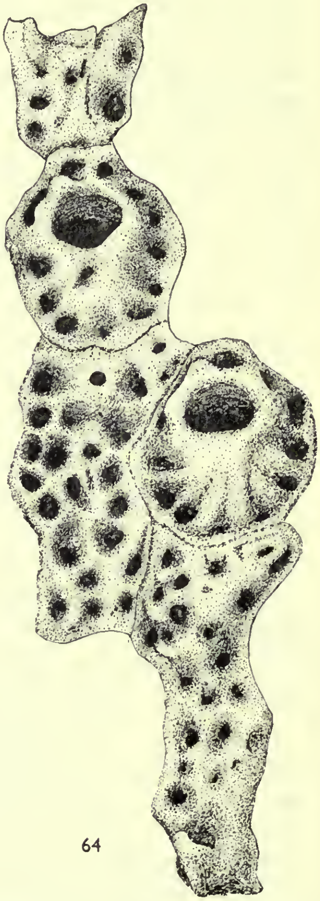

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Figs. 62–64. Fig. 62. *Tubucella mamillaris* (Milne Edwards). D.48772. Outline of a zoarial fragment. Fig. 63. *Tubucella mamillaris* (Milne Edwards). D.48773. Five ordinary zooecia. Fig. 64. *Tubucella mamillaris* (Milne Edwards). D.48774. Two ovicelled zooecia and a small portion of a third, distal one.

bordered laterally and distally by a crown of 12 large pores. Free peristome short, longitudinally costate, with a slightly widened secondary orifice.

Avicularia lacking.

MEASUREMENTS :

Ordinary zooecia

Lz (7) 0·812 (0·0780) mm., 0·67–0·90 mm.
lz (7) 0·211 (0·0269) mm., 0·17–0·24 mm.
ho (7) 0·100 (0·0146) mm., 0·09–0·12 mm. } secondary orifice
lo (7) 0·106 (0·0190) mm., 0·09–0·13 mm. } secondary orifice
Length of peristome (7) 0·478 (0·0726) mm., 0·38–0·52 mm.

Ovicelled zooecia

ho (5) 0·099 (0·0076) mm., 0·09–0·11 mm. } secondary orifice
lo (5) 0·144 (0·0112) mm., 0·14–0·16 mm. } secondary orifice
Length of peristome (5) 0·333 (0·0200) mm., 0·30–0·35 mm.

DISTRIBUTION. Eocene (Lutetian, Auversian) ; France, Belgium. Oligocene (Stampian) ; France. Miocene (Aquitanian) ; France.

Family **ADEONIDAE** Hincks

Genus ***TEICHOPORA*** Gregory

1893 *Teichopora* Gregory : 249.
?1907*b* *Poristoma* Canu : 154.

TYPE SPECIES (by monotypy). *Teichopora clavata* Gregory 1893 : 249, pl. 31, figs. 5–7. Eocene (Bartonian) ; Barton Clay, Barton, Hampshire.

DIAGNOSIS. Frontal wall calcareous, smooth or granular, with single row of areolae continuing round distal margin. No ascopore or spiramen. Orifice sub-circular, with broad, U-shaped sinus proximally, without condyles. Peristome long enough to hide orifice, but immersed in thick frontal. Secondary orifice sub-circular, unmodified. Avicularia adventitious, small, single or paired, placed on proximo-lateral margins of orifice, becoming enclosed in thickening peristome so as to be nearly invisible exteriorly. Additional small, circular avicularia sometimes scattered over frontal. Gonoecia probably not of different form from zooecia. Zoarium erect, bilaminar, arborescent.

REMARKS. This genus has been poorly understood because its oral structure has never been clarified. Gregory (1893 : 249) described the orifice of the type species as simple and sub-circular, but he did not differentiate between the primary and secondary orifices. Actually, the orifices in the holotype (49733, Edwards Collection) are so filled with quartz grains that the structure of the primary orifice is completely obscured, but a paratype on the same slide, however poorly preserved in other respects, has a well-preserved orifice with a sinus but without condyles.

Canu & Caillot (1932 : 12), Canu (1926 : 456, 457), Davis (1934 : 228, 229), and Dartevelle (1933 : 108 ; 1936 : 29) all have confused *Teichopora* with *Bracebridgia*

MacGillivray. *Mucronella pyriformis* Busk, the Recent Indo-Pacific type species of *Bracebridgia* (lectotype, Department of Zoology, British Museum (Natural History), 87.12.9.615, Challenger Collection), differs from the European and British Eocene species in having a non-sinuate, semi-circular orifice with a short, broad lyrula occupying almost the entire proximal margin; and vicarious, rather than adventitious avicularia. These differences are usually considered to be of generic magnitude in the Adeonidae; therefore, the species exemplified by *T. clavata* and including at least *Eschara syringopora* Reuss in addition (see Waters 1891 : 20, pl. 3, figs. 2–4) must be excluded from *Bracebridgia*.

Canu (1907*b* : 154) introduced the genus *Poristoma* (consistently misspelt "*Porostoma*" in later works) for Adeonidae having "an avicularium developed in the peristomie or on the peristome" (translation). He listed under this generic name one *nomen nudum* (*Poristoma parisiensis*), one new species (*P. incisa*), and two species previously described (*T. clavata* Gregory and *Eschara polymorpha* Reuss). Selection of a type species for *Poristoma*, apparently an action that has not yet been taken, should be contingent upon a detailed study of *P. incisa* and *E. polymorpha*. Should *T. clavata* be chosen as type species, *Poristoma* would, of course, become an objective synonym of *Teichopora*.

Another genus which might be confused with *Teichopora* is *Meniscopora* Gregory, the type species of which, *M. bigibbera* Gregory (1893 : 251, pl. 31, figs. 8, 9; holotype 49732, Edwards Collection) from the Lower Bracklesham Beds, differs from *Teichopora* in having oral condyles and the avicularium always outside the peristome.

Teichopora clavata Gregory

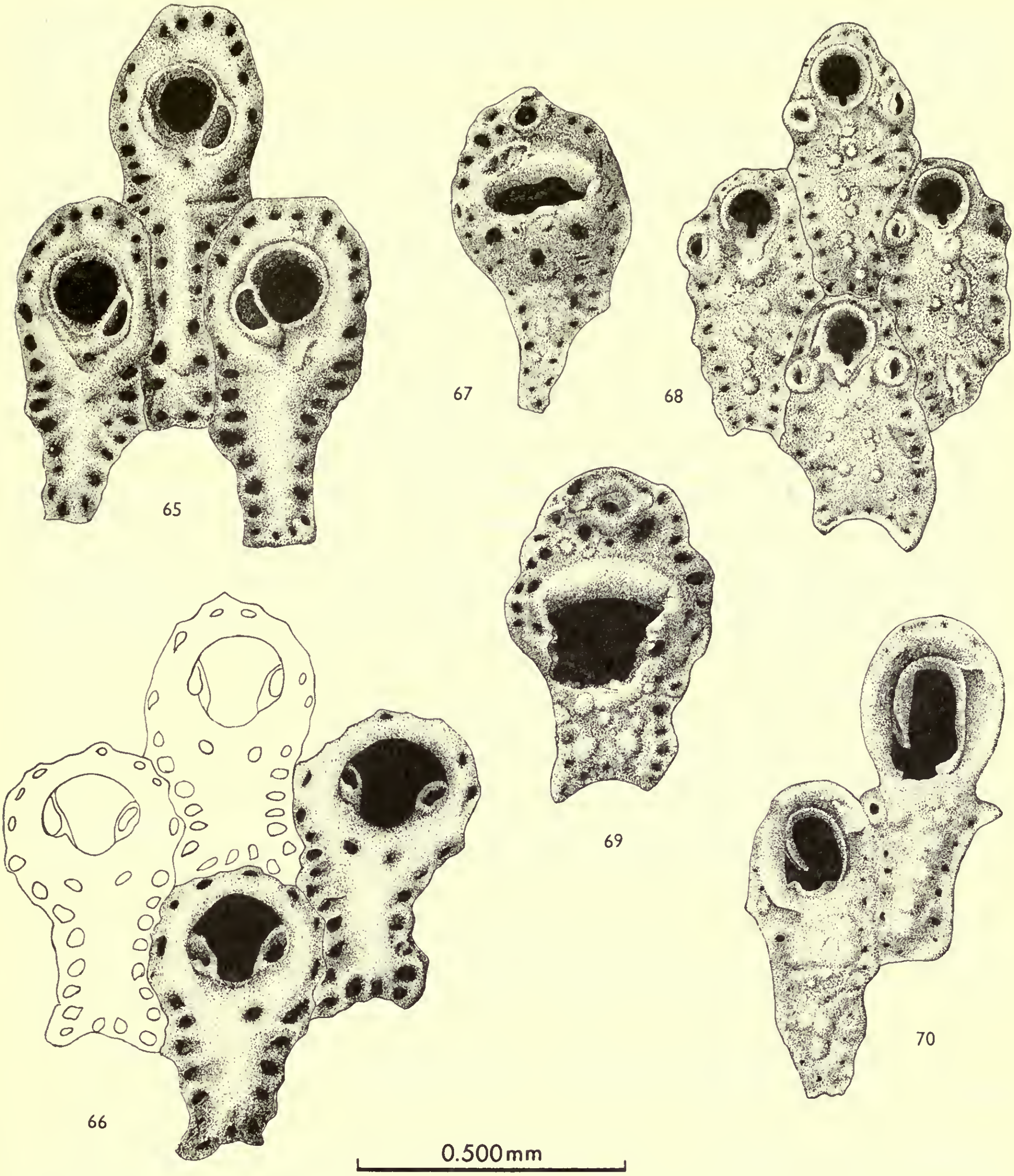
(Text-figs. 65, 66)

1893 *Teichopora clavata* Gregory : 249, pl. 31, figs. 5–7.
1907*b* *Poristoma clavata* (Gregory) Canu : 155, pl. 20, figs. 14, 15.
1925 *Bracebridgia clavata* (Gregory) Canu : 47.
1926 *Bracebridgia gyrinus* Canu : 756, pl. 28, figs. 3–6.
?1926 *Bracebridgia grandis* Canu : 757, pl. 28, figs. 1, 2.
1929 *Teichopora clavata* Gregory; Burton : 328.
?1929*a* *Bracebridgia grandis* Canu; Canu & Bassler : 49.
1933 *Bacebridgia* [sic] *gyrinus* Canu; Dartevelle : 108.
?1933 *Bacebridgia* [sic] *grandis* Canu; Dartevelle : 108.
1933 *Meniscopora clavata* (Gregory) Dartevelle : 114.
1936 *Bacebridgia* [sic] *gyrinus* Canu; Dartevelle : 29.
?1936 *Bacebridgia* [sic] *grandis* Canu; Dartevelle : 29.
1946 *Bracebridgia clavata* (Gregory); Buge : 436.

HOLOTYPE. 49733, Edwards Collection. Barton Clay; Barton, Hants. Figured by Gregory (1893, pl. 31, fig. 5).

FIGURED SPECIMENS. D.48781 (Text-fig. 65), D.48782 (Text-fig. 66).

ADDITIONAL MATERIAL. Seventeen specimens, D.48783–D.48799.



FIGS. 65–70. Fig. 65. *Teichopora clavata* Gregory. D.48781. Three zooecia with single avicularium. Fig. 66. *Teichopora clavata* Gregory. D.48782. Four zooecia with paired avicularia. Fig. 67. *Schizostomella curryi* sp. nov. D.48800. Holotype. Nearly complete gonoecium. Fig. 68. *Schizostomella curryi* sp. nov. D.48801. Paratype. Four ordinary zooecia. Fig. 69. *Schizostomella curryi* sp. nov. D.48802. Paratype. Broken gonoecium. Fig. 70. *Schizostomella curryi* sp. nov. D.48803. Paratype. Two avicularian zooecia.

DIAGNOSIS. *Teichopora* with the oral avicularia either single or paired, but never meeting across the secondary orifice, the rostrum directed distally and slightly outwards.

DESCRIPTION. *Zoarium* erect, arborescent, bilaminar, compressed, composed of longitudinal rows of zooecia, those in adjacent rows alternating in position.

Zooecia club-shaped, separated by very faint furrows. Length more than twice width. Frontal wall thick, strongly convex, with a prominent median longitudinal ridge connecting secondary orifice with proximal margin of zooecium. Frontal surface finely granular, with a single row of 20–30 large areolae evenly spaced round entire margin, and one or two additional pits just proximal to peristome on heavily calcified zooecia.

Orifice sub-circular to oval, the distal margin broadly rounded, the proximal margin curved to a slightly shorter radius to form a broad, median sinus. Peristome erect, not hiding distal areolae, very thick, long enough to hide orifice, but immersed in thickened frontal. Secondary orifice sub-circular, unmodified.

Avicularia adventitious, single or paired, placed on peristome at proximo-lateral margin of orifice, becoming enclosed by peristome as calcification advances. Rostrum rounded, directed distally and slightly outwards. Pivotal structure lacking.

Gonoecia, if present, not sufficiently differentiated from zooecia to be recognizable ; zooecia with paired avicularia and slightly enlarged secondary orifice may be gonoecia.

MEASUREMENTS :

Zooecia with single avicularium

Lz	(5) 0·734 (0·0229) mm., 0·71–0·76 mm.	
lz	(5) 0·277 (0·0143) mm., 0·26–0·30 mm.	
ho	(5) 0·132 (0·0115) mm., 0·12–0·14 mm.	secondary orifice
lo	(5) 0·126 (0·0153) mm., 0·11–0·14 mm.	
Lav	(5) 0·106 (0·0130) mm., 0·09–0·13 mm.	

Zooecia with paired avicularia

Lz	(5) 0·530 (0·0264) mm., 0·50–0·54 mm.	
lz	(5) 0·311 (0·0155) mm., 0·29–0·33 mm.	
ho	(5) 0·156 (0·0127) mm., 0·14–0·17 mm.	secondary orifice
lo	(5) 0·169 (0·0195) mm., 0·14–0·19 mm.	
Lav	(5) 0·075 (0·0094) mm., 0·07–0·09 mm.	

REMARKS. Canu (1926 : 757) separated the specimens from the French Auversian that he had previously identified with *T. clavata* and gave them the new name *B. grandis* because of their larger zooecia and orifices. At the same time he (1926 : 756) described *B. gyrinus* as a new species differing from *B. grandis* " only in its smaller dimensions and not regularly elliptical orifice " (translation). *B. gyrinus* thus appears to be a synonym of *T. clavata*, and *B. grandis* probably is also.

The holotype of *T. clavata* has its orifices filled with quartz grains, but the oral avicularium appears to be visible in one zooecium. The " gonoecia " described and illustrated by Gregory (1893 : 249, pl. 31, fig. 6) in paratype 49757, Edwards Collection, seem to be frontally thickened ordinary zooecia from near the zoarial base.

T. syringopora (Reuss) differs from *T. clavata* principally in having the oral avicularia always paired and their rostra directed transversely inwards so that they frequently meet across the proximal part of the secondary orifice making a false ascopore (see Waters 1891 : pl. 3, figs. 2, 3).

DISTRIBUTION. Eocene (Ypresian, Lutetian, Bartonian) ; France. Eocene (Auversian) ; England, ?Belgium. Eocene (Bartonian) ; England.

Genus ***SCHIZOSTOMELLA*** Canu & Bassler

1908 *Schizostoma* Canu : 69 (*non* Bronn 1834).
1927 *Schizostomella* Canu & Bassler : 20, 38.

TYPE SPECIES (by original designation). *Schizostoma crassum* Canu 1908 : 70, pl. 8, figs. 6–8. Eocene (Lutetian) ; vicinity of Paris, France.

DIAGNOSIS. Frontal wall calcareous, finely granular to coarsely tuberculate or with large, irregular gibbosities. Areolae in one row or two, the outer one continuing round distal margin. Orifice oval, with distinct median-proximal sinus, deep and usually narrow, sometimes limited by small condyles. Peristome thick, becoming immersed in thickened frontal. Secondary orifice oval, without sinus. Avicularia adventitious, frontal, single or paired, placed on lateral margins of zooecium, usually near orifice, sometimes on distal portion of gonoecium. Rostrum rounded, cross-bar or condyles lacking. Vicarious avicularia, modified from ordinary zooecia by oral enlargement, present in some species. Gonoecia larger than zooecia, with wide, elliptical orifice, single or multiple ascopore (rarely lacking), and swollen distal portion with imperforate, marginally areolate surface.

REMARKS. This characteristic British and European Tertiary genus has not yet been found in the New World. The following species, in addition to the type and *S. curryi* sp. nov. and *S. liancourti* (Canu) described below, seem to have been referred correctly to *Schizostomella* :

Schizostoma aviculiferum Canu (1908 : 71, pl. 8, fig. 12), Lutetian ; France.

Schizostoma denticulatum Canu (1908 : 72, pl. 7, figs. 14–16), Ypresian–Lutetian ; France.

Escharellina parnensis d'Orbigny (Canu 1908 : 74, pl. 8, figs. 14–16), Lutetian ; France.

Schizoporella magnoaperta Gregory (1893 : 239, pl. 33, fig. 9), London Clay ; Sheppey, Kent. Barton Beds ; Barton, Hants. Auversian ; France.

Eschara socialis Busk (Lagaaij 1952 : 120, pl. 13, figs. 4, 5, 7, 8), Coralline Crag ; Suffolk. Pliocene ; Holland.

Schizostoma gibbosum Canu (Buge 1957 : 296), Miocene and Pliocene ; France.

Schizostoma helveticum Canu & Lecointre (Buge 1957 : 297), Miocene and Pliocene ; France.

Eschara heteromorpha Reuss (Canu 1914*b* : 472, pl. 14, figs. 1–4, who erroneously referred it to *Metrarabdotos*), Oligocene ; France.

1. ***Schizostomella curryi***[11] sp. nov.

(Text-figs. 67–70)

HOLOTYPE. D.48800 (Text-fig. 67).

PARATYPES. D.48801 (Text-fig. 68), D.48802 (Text-fig. 69), D.48803 (Text-fig. 70) ; D.48804–D.48905 (102 specimens) ; L.S.U. 8038.

DIAGNOSIS. *Schizostomella* with relatively large zooecia having gibbosities and 24–28 areolae ; frontal avicularia usually paired, slightly removed from orifice ; vicarious avicularia little modified from zooecia ; gonoecia with a small distal avicularium and a single, median ascopore.

DESCRIPTION. *Zoarium* erect, arborescent, branching, composed of compressed, bilaminar fronds, with zooecia arranged in as many as 12 longitudinal rows, those in adjacent rows alternating in position. Number of zooecial rows increases distally by bifurcation. Base of zoarium small, encrusting.

Zooecia rhomboidal to club-shaped, very regularly arranged, not distorted round the gonoecia, separated by a faint groove. Communication between zooecia of the same series and adjacent series by simple pores placed in a single line of 14–16 near base of distal and disto-lateral walls. Zooecial length nearly twice width. Frontal surface finely granular, with larger gibbosities especially on central portion. Areolae small and circular proximally and laterally, smaller and slit-like distally, disposed in a single, evenly spaced row of 24–28 entirely round zooecial margin. Interareolar costules, where present, limited to periphery.

Orifice nearly terminal on frontal surface, small, not inclined to frontal plane. Distal portion semi-circular, with evenly rounded, smooth margin. Proximal portion straight, but interrupted medially in a deep, V-shaped or linear sinus. Peristome thin and short, never standing much above frontal surface nor obscuring primary orifice from frontal view. Secondary orifice oval, larger than primary one.

Avicularia dimorphic : small, adventitious and large, vicarious. Adventitious avicularia usually paired, rarely single or absent, placed on lateral corners of frontal wall over one or two areolae, having rounded rostra and lacking pivotal bar or condyles. Vicarious avicularia rare and sporadic, developed from zooecia by enlargement of orifice and oral region to greatly varying degrees. Avicularian orifice with broad distal shelf and greatly widened sinus flanked by small lateral condyles.

Gonoecia slightly longer and broader than ordinary zooecia, with small, paired, adventitious avicularia developed proximally and laterally to orifice and a third, small avicularium placed medially on distal margin. Gonoecial orifice a very wide ellipse separated from the single, rounded ascopore. Oral region strongly raised, the post-oral portion with a distal marginal crown of enlarged areolae, but not otherwise ornamented.

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[11] After Mr. Dennis Curry.

MEASUREMENTS :

Ordinary zooecia

Lz	(10)	0·496	(0·0442) mm.,	0·41–0·56 mm.
lz	(10)	0·239	(0·0171) mm.,	0·21–0·26 mm.
ho	(10)	0·090	(0·0101) mm.,	0·08–0·11 mm.
lo	(10)	0·088	(0·0107) mm.,	0·08–0·11 mm.
Lav	(9)	0·070	(0·0153) mm.,	0·05–0·09 mm.

Gonoecia

Lz	(5)	0·590	(0·0200) mm.,	0·57–0·62 mm.
lz	(5)	0·332	(0·0398) mm.,	0·27–0·38 mm.
ho	(4)	0·051	(0·0099) mm.,	0·04–0·06 mm.
lo	(5)	0·188	(0·0326) mm.,	0·17–0·21 mm.
Lav	(6)	0·067	(0·0219) mm.,	0·05–0·10 mm.

Avicularian zooecia

Lz	(3)	0·616	(0·0342) mm.,	0·58–0·65 mm.
lz	(3)	0·222	(0·0308) mm.,	0·20–0·26 mm.
ho	(4)	0·165	(0·0214) mm.,	0·14–0·19 mm.
lo	(4)	0·132	(0·0204) mm.,	0·11–0·15 mm.

REMARKS. The avicularian zooecia of this species are like the B-zooecia of *Steganoporella* in relation to the ordinary zooecia. It is, of course, possible that they represent a form of dimorphism different from avicularian, but the oral enlargement, markedly different from that of the gonoecia, is almost certainly a concomitant of opercular enlargement for presumably the same function as the development of avicularian mandibles.

S. curryi is very close to *S. gibbosa* (Canu), a French Miocene and Pliocene species, from which it differs in having avicularian zooecia and in having the gonoecia with a distal avicularium and a single, median ascopore.

2. ***Schizostomella liancourti*** (Canu)

(Text-figs. 71, 72)

1908 *Schizostoma liancourti* Canu : 72, pl. 22, figs. 10, 11.
1946 *Schizostomella liancourti* (Canu) Buge : 438.

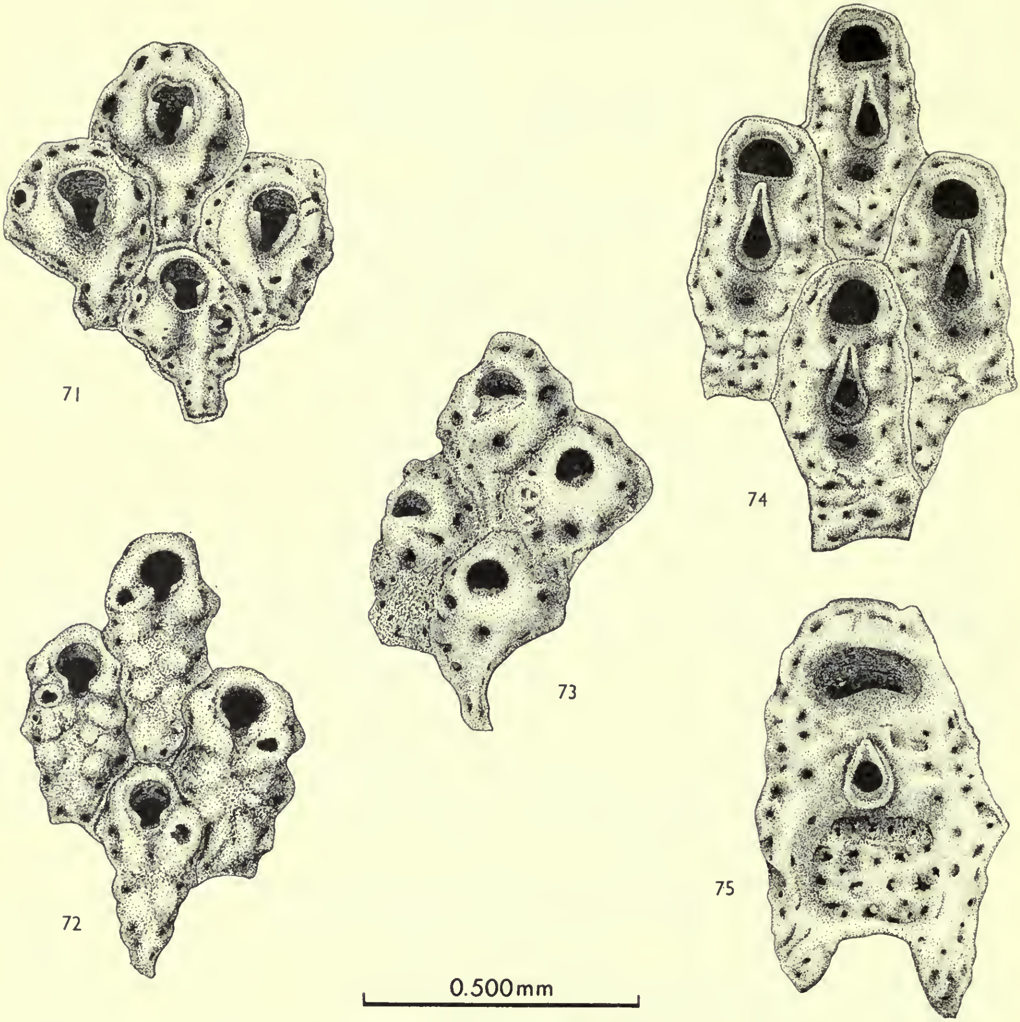
FIGURED SPECIMENS. D.48906 (Text-fig. 71), D.48907 (Text-fig. 72).

ADDITIONAL MATERIAL. Five specimens, D.48908–D.48912.

DIAGNOSIS. *Schizostomella* with relatively small zooecia having tuberculate frontal walls with 14–20 areolae ; secondary orifice elongate, constricted at middle ;

frontal avicularia small, usually single, placed on peristome; vicarious avicularia lacking; gonoecium (*fide* Canu 1908 : 72) without distal avicularium or ascopore.

Description. *Zoarium* erect, arborescent, branching, composed of compressed, bilaminar fronds originating from a small, encrusting base. Zooecia arranged in 6–12 longitudinal rows on each side of frond, those in adjacent rows alternating in position.



Figs. 71–75. Fig. 71. *Schizostomella liancourti* (Canu). D.48906. Four heavily calcified zooecia. Fig. 72. *Schizostomella liancourti* (Canu). D.48907. Four lightly calcified zooecia. Fig. 73. *Adeonellopsis selseyensis* sp. nov. D.48913. Holotype. Two gonoecia (on the left) and two zooecia. Fig. 74. *Adeonellopsis punctata* (Canu). D.48914. Four zooecia. Fig. 75. *Adeonellopsis punctata* (Canu). D.48915. Gonoecium.

Zooecia club-shaped, very regularly arranged, separated by a shallow groove. Communication between zooecia by simple pores. Zooecial length about one and a half times width. Frontal wall thick, convex, becoming flat with age, highest at proximo-lateral corners of orifice. Frontal surface tuberculate in thin-walled zooecia, becoming finely granular as wall thickens. Areolae small, circular, nearly occluding as calcification progresses, slit-like round distal margin, disposed in a single, evenly spaced row of 14–20 entirely round zooecial margin. Interareolar costules lacking.

Orifice sub-terminal on frontal surface, small, not inclined to frontal plane. Distal portion evenly rounded, smooth, semi-circular. Proximal portion nearly straight, interrupted medially in a deep but broad, U-shaped sinus. Peristome very thick, never standing much above frontal surface, but obscuring primary orifice from frontal view. Secondary orifice larger than primary one, constricted at middle so as nearly to form a spiramen.

Avicularia monomorphic, adventitious, usually single, rarely paired or multiple, placed on peristome near proximo-lateral corners of orifice, or on lateral margins of frontal wall, over one or two areolae. Rostrum rounded. Pivotal structures lacking.

Gonoecia lacking in material at hand.

MEASUREMENTS :

Lz	(10)	0·355 (0·0418) mm.,	0·30–0·43 mm.	
lz	(10)	0·216 (0·0335) mm.,	0·17–0·26 mm.	
ho	(9)	0·089 (0·0172) mm.,	0·07–0·12 mm.	secondary orifice
lo	(11)	0·078 (0·0092) mm.,	0·07–0·09 mm.	
Lav	(7)	0·077 (0·0131) mm.,	0·05–0·09 mm.	

REMARKS. This species, hitherto known only from the French Lutetian, is easily distinguished from other species of *Schizostomella* by its constricted secondary orifice and its thick perstome on which the avicularia are placed. *S. crassa* (Canu) has a similar peristome, but its secondary orifice is different, and its frontal avicularium is well removed from the peristome. Canu (1908 : 72) characterized *S. liancourti* as always having paired or multiple avicularia, but his own illustrations (1908 : pl. 22, figs. 10, 11) show zooecia with single avicularium.

DISTRIBUTION. Eocene (Lutetian) ; France.

Genus *ADEONELLOPSIS* MacGillivray

Adeonellopsis selseyensis sp. nov.

(Text-fig. 73)

HOLOTYPE. D.48913 (Text-fig. 73).

DIAGNOSIS. *Adeonellopsis* with small, rhombic zooecia ; primary orifice visible in frontal aspect, proximal lip serrate ; ascopore simple or compound with as many as

5 perforations; avicularia frontal, paired lateral and occasionally single distal as well; gonoecia differ only slightly in size, shape, and oral structure from zooecia.

Description. *Zoarium* erect, arborescent, composed of compressed, bilaminar fronds with more than 7 longitudinal rows of zooecia on each side, the zooecia in adjacent rows alternating in position.

Zooecia rhombic, approximately equilateral, separated by distinct furrows. Length and width sub-equal. Frontal wall thick, markedly convex, highest round the proximal lip of the orifice. Frontal surface very finely granular, without tubercles or costules, margined by a single row of 18–20 small, circular areolae evenly spaced round the whole periphery. Ascopore placed just proximal to mid-length in a small, median pit, simple or compound, formed of a small circular disc with 2–5 minute perforations.

Orifice removed slightly from distal end of frontal surface, small, semi-circular, surrounded by a thick peristome, but not hidden from frontal view. Distal margin evenly rounded, smooth; proximal margin nearly straight, finely serrated. Peristome not elevated above frontal surface. Secondary orifice sub-circular.

Avicularia adventitious, frontal, small, multiple, their rostra rounded or slightly attenuated; pivotal structures lacking. One pair of avicularia present on each zooecium and gonoecium, one in each lateral corner; rostra directed inwards and slightly distally or proximally. An additional unpaired avicularium with rounded rostrum present on a few zooecia and gonoecia, placed on the distal part of the peristome, either on the mid-line or slightly to one side. Vicarious avicularia unknown.

Gonoecia slightly wider and longer than zooecia. Frontal wall like that of zooecia but more swollen round orifice. Ascopore, areolae, and avicularia similar to those of zooecia. Orifice slightly wider and shorter than that of zooecia, but with similar serration of proximal lip.

Measurements:

Zooecia

Lz	(5) 0·282 (0·0264) mm., 0·26–0·33 mm.	
lz	(5) 0·231 (0·0148) mm., 0·22–0·26 mm.	
ho	(5) 0·056 (0·0047) mm., 0·05–0·06 mm.	secondary orifice
lo	(5) 0·067 (0·0038) mm., 0·06–0·07 mm.	
Lav	(5) 0·044 (0·0038) mm., 0·04–0·05 mm.	

Gonoecia

Lz	(4) 0·355 (0·0110) mm., 0·34–0·38 mm.	
lz	(4) 0·250 (0·0214) mm., 0·22–0·27 mm.	
ho	(4) 0·043 (0·0000) mm., 0·04 mm.	secondary orifice
lo	(4) 0·081 (0·0049) mm., 0·08–0·09 mm.	
Lav	(4) 0·047 (0·0049) mm., 0·04–0·05 mm.	

Adeonellopsis punctata (Canu)

(Text-figs. 74, 75)

1907*b* *Adeonella punctata* Canu : 149, pl. 20, fig. 2.
1920 *Cribricella punctata* (Canu) Canu & Bassler : 564.
1946 *Adeonella punctata* Canu ; Buge : 436.
1960 *Adeonella punctata* Canu ; Balavoine : 246.
1963 " *Adeonellopsis punctata* (Reuss) " Malecki : 128, pl. 14, fig. 4.

FIGURED SPECIMENS. D.48914 (Text-fig. 74), D.48915 (Text-fig. 75).

ADDITIONAL MATERIAL. Forty-three specimens, D.48916–D.48959.

DIAGNOSIS. *Adeonellopsis* with large, rhomboidal zooecia ; primary orifice hidden from frontal view, the proximal lip smooth ; ascopore single and simple on zooecia, large and compound on gonoecia, with more than 20 perforations ; avicularium frontal, single, median, between orifice and ascopore, the rostrum directed distally ; gonoecia much larger than zooecia, the orifice greatly widened.

DESCRIPTION. *Zoarium* erect, arborescent, branching, composed of compressed, bilaminar fronds, originating from a small, encrusting base, expanding rapidly to as many as 20 longitudinal rows of zooecia on each side. Zooecia of adjoining rows alternate in position ; new rows added distally by intercalation.

Zooecia elongate, rhomboidal, variable in size and shape, but not distorted round gonoecia, separated by a furrow. Length nearly two-and-a-half times width. Frontal wall thick, only slightly convex, the area round the ascopore depressed. Surface finely granular, sometimes with small tubercles, margined entirely by a single, evenly spaced row of 20–30 small, circular areolae. Scattered areolae of a second, inner row sometimes present proximal to peristome and at proximal end of zooecium. Ascopore single, simple, circular, small, placed just proximal to mid-length in a very deep depression.

Orifice just short of distal end of zooecium, small, semi-circular, hidden by peristome from frontal view. Distal margin evenly rounded ; proximal margin nearly straight, smooth. Peristome thick, elongate, but generally buried in the frontal so that only distal and lateral portions are raised, sometimes enough to form a hood-like projection over orifice. Secondary orifice about same size and shape as primary one.

Avicularium adventitious, frontal, placed between orifice and ascopore, with rostrum directed distally, either longitudinally or slightly obliquely. Rounded end of avicularium stops short of ascopore-pit, and rostrum does not quite reach peristome. Rostrum raised, pointed, slightly channelled. Pivotal structure lacking.

Gonoecium slightly longer than and about twice as wide as zooecium. Frontal wall swollen all round orifice, with additional rows of areolae developed proximal to orifice. Ascopore greatly enlarged, compound, consisting of a flat, roughly circular disc perforated by 20 or more small pores. Orifice wider than that of zooecium, the proximal lip distinctly convex. Avicularium smaller than that of zooecium.

MEASUREMENTS :

Zooecia

Lz	(10) 0·508 (0·0689) mm., 0·43–0·62 mm.	
lz	(10) 0·210 (0·0198) mm., 0·19–0·24 mm.	
ho	(10) 0·080 (0·0099) mm., 0·06–0·09 mm.	secondary orifice
lo	(10) 0·091 (0·0070) mm., 0·09–0·10 mm.	
Lav	(10) 0·160 (0·0285) mm., 0·13–0·22 mm.	

Gonoecia

Lz	(2) 0·573 (0·0363) mm., 0·55–0·60 mm.	
lz	(2) 0·423 (0·0665) mm., 0·38–0·47 mm.	
ho	(2) 0·077 (0·0121) mm., 0·07–0·09 mm.	secondary orifice
lo	(2) 0·197 (0·0121) mm., 0·19–0·20 mm.	
Lav	(2) 0·124 (0·0181) mm., 0·11–0·14 mm.	

REMARKS. This species does not appear to be the same as the German Oligocene species reported by Reuss (1865 : 649, pl. 12, figs. 1, 2) as *Eschara coscinophora* Reuss and placed in synonymy with *A. punctata* by Canu (1907*b* : 149). *E. coscinophora* from the Miocene of Austria is conspecific with *E. imbricata* Philippi according to Lagaaij (1952 : 120). Therefore, the synonymy given by Malecki (1963 : 128) is too inclusive.

The generic assignment of *A. punctata* is difficult to make. The presence of an ascopore rather than a spiramen excludes it from *Adeonella* Busk (see Harmer 1957 : 802). Three genera of Adeonidae have well-developed ascopores : *Adeona* Lamouroux, *Adeonellopsis* MacGillivray, and *Reptadeonella* Busk. Harmer (1957 : 789–802, 814–818) differentiated these genera principally upon zoarial characters, at least some of which are not always evident in fragmentary fossil material. Cheetham & Sandberg (1964 : 1039) characterized *Reptadeonella* as having a simple, single or rarely double ascopore on both zooecia and gonoecia ; a sub-oral, median avicularium directed transversely or longitudinally or obliquely distally, its rostrum reaching the peristome ; occasionally additional frontal avicularia near the proximal margin of the zooecium ; and gonoecia with wide, short secondary orifice but not otherwise differentiated from the zooecia.

The type species of *Adeona*, *A. grisea* Lamouroux (chosen by Gregory 1893), represented in the Department of Zoology, British Museum (Natural History) by specimens such as 99.7.1.2750 and 2753, Busk Collection, has a simple, single or double ascopore on both zooecia and gonoecia ; a single, frontal avicularium flanking the ascopore distally and directed transversely or obliquely distally, its rostrum not reaching the peristome ; and gonoecia larger than the zooecia, with short, wide orifices.

Adeonellopsis seems to be much more variable than the other two ascopore-bearing Adeonid genera. The type species, *A. foliacea* MacGillivray (chosen by Canu & Bassler 1917), represented in the Department of Zoology, British Museum (Natural History) by specimen 97.5.1.709, has a compound ascopore on both zooecia and gonoecia ; multiple sub-oral avicularia, both median and lateral, none with rostra reaching the peristome, on the zooecia ; supra-oral avicularia additionally on the gonoecia ; and gonoecia larger than the zooecia, with widened orifices.

Because of its compound gonoecial ascopore, *A. punctata* seems to fit best in *Adeonellopsis*, even though it has a single sub-oral avicularium and a simple zooecial ascopore. In these respects it resembles *Adeonellopsis arculifera* (Canu & Bassler) and *A. parvipuncta* MacGillivray (see Harmer 1957 : pl. 56, figs. 13, 14, 16).

Distribution. Eocene (Lutetian) ; France. Eocene (Ludian) ; Poland.

Family **CELLEPORINIDAE** Harmer

Genus ***CELLEPORINA*** Gray

Celleporina thomasi[12] sp. nov.

(Text-figs. 76, 77)

Holotype. D.48960 (Text-fig. 76).

Paratypes. D.48961 (Text-fig. 77) ; D.48962–D.48970 (9 specimens) ; L.S.U. 8039.

Diagnosis. *Celleporina* with median sub-oral avicularium on a prominent umbo and with lateral-oral bosses ; distal hood of ovicell forming a narrow rim within which is a row of small, marginal pores.

Description. *Zoarium* encrusting, unilaminar, the zooecia arranged in irregular longitudinal rows, those in adjacent rows alternating in position. Portions of zoaria probably rose as unilaminar tubes from the substrate.

Zooecia irregularly rhomboidal, separated by narrow, raised threads with a faint groove at the crest. Length almost twice width. Frontal wall thin, nearly flat except at sub-oral umbo. Surface tuberculate, radially striated, with large, circular areolae in a single marginal row of 4–6 on each side and usually an additional 2–3 proximally. Interareolar costules weak, peripheral. Sub-oral umbo, lacking on a few zooecia, usually massive.

Orifice commonly partly obscured in frontal view by proximal umbo and lateral bosses, oval, the distal portion semi-circular, the proximal portion a deep, wide, rounded sinus between a pair of rudimentary, widely spaced, lateral condyles. Peristome an irregular distal ridge, not differentiated from frontal surface, thick, smooth, terminating on each side of the orifice in a tubercle which enlarges to form a boss with advancing calcification, and which connects with the sub-oral umbo.

Avicularium adventitious, sometimes lacking, single, median, sub-oral, placed on the umbo, sometimes facing into the peristome, but with rostrum directed frontally, proximally, and usually slightly to one side. Rostrum rounded ; pivotal bar complete.

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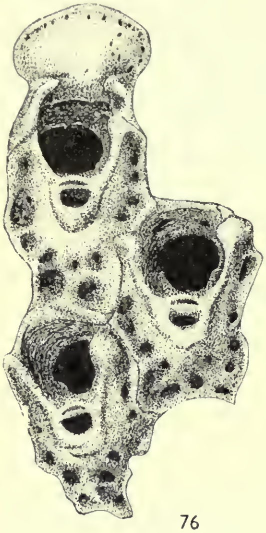
[12] After Dr. H. Dighton Thomas.



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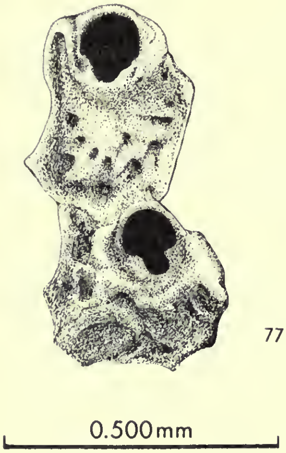

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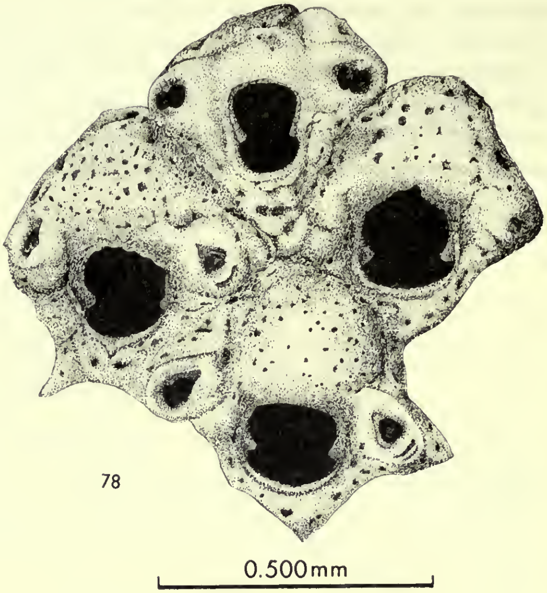

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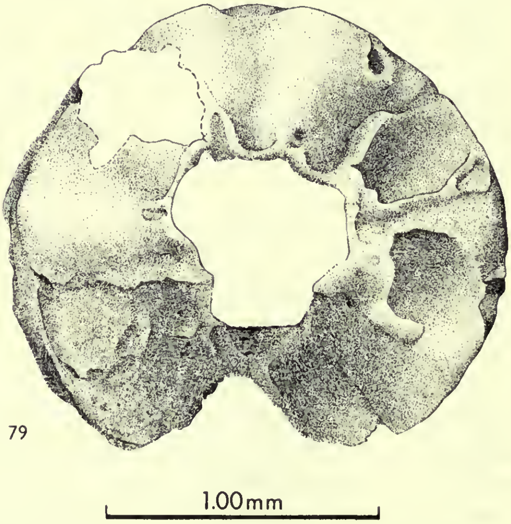

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Figs. 76–79. Fig. 76. *Celleporina thomasi* sp. nov. D.48960. Holotype. Three heavily calcified zooecia, all with oral avicularia and one with an ovicell. Fig. 77. *Celleporina thomasi* sp. nov. D.48961. Paratype. Two lightly calcified zooecia lacking avicularia. Fig. 78. *Kionidella hastingsae* sp. nov. D.48971. Holotype. Four zooecia, three with ovicells. Fig. 79. *Kionidella hastingsae* sp. nov. D.48972. Paratype. Basal view of a hollow zoarial fragment.

Ovicell hyperstomial, globular, wider than long ; surface irregularly tuberculate, with a smooth, raised distal rim within which is a marginal row of small pores. Additional pores sometimes scattered over the surface. Proximal margin of ovicell generally visible between peristomial ridges which extend on to its surface.

MEASUREMENTS :

Lz (10) 0·397 (0·0513) mm., 0·36–0·50 mm.
lz (10) 0·221 (0·0224) mm., 0·19–0·26 mm.
ho (10) 0·115 (0·0157) mm., 0·09–0·14 mm.
lo (10) 0·101 (0·0054) mm., 0·09–0·11 mm.
Lav (10) 0·092 (0·0079) mm., 0·09–0·10 mm.
Lov (6) 0·167 (0·0105) mm., 0·15–0·18 mm.

REMARKS. This species, the oldest referred to *Celleporina*, differs from Recent species of the genus in having the ovicell with numerous pores and without the hood-like extension of the distal rim, and in having the frontal avicularium median sub-oral rather than lateral. The lateral oral bosses may foreshadow the lateral columnar avicularia so characteristic of later species. Otherwise the Upper Bracklesham species fits well in *Celleporina*.

Family **MAMILLOPORIDAE** Canu & Bassler

Genus ***KIONIDELLA*** Koschinsky

1885 *Kionidella* Koschinsky : 67.

TYPE SPECIES (chosen by Canu & Bassler 1929*b*). *K. excelsa* Koschinsky 1885 : 68, pl. 7, figs. 5–12. Eocene (Lutetian) ; Bavaria.

DIAGNOSIS. Frontal wall calcareous, smooth or granular, without pores or areolae. Orifice elongate, with lateral condyles and a thin, smooth peristome. Avicularia adventitious, single or paired, lacking on some zooecia, placed on lateral margins of frontal, with long or short rostrum directed inwards. Zooecia erect, prismatic, with just orifice and small area of frontal wall showing on frontal surface, communicating by simple pores placed low in zooecial walls. Zoarium hollow, tubular, unilaminar, ancestrular end closed, and distal ends of zooecia directed towards distal margin of zoarium. Ovicell hyperstomial, large, not raised above zoarial surface.

REMARKS. The presence of ovicells in *Kionidella* was first noted by Waters in the type species (1891 : 29, pl. 4, fig. 6). Canu (*in* Buge 1946 : 438) later misinterpreted the ovicell as intermediate between entozooecial and entotoichal. Waters's figure indicates, and the specimens of *K. hastingsae* sp. nov. described below substantiate, that the ovicell of this genus is hyperstomial but deeply immersed, similar to that of *Mamillopora*.

Canu & Bassler (1929*b* : 477) placed *Kionidella* in synonymy with *Discoflustrellaria*, a genus founded by d'Orbigny (1853 : 508) for three species : *D. dactylus* d'Orbigny (1853 : 508, not figured) from the Lutetian of France ; *D. clypeiformis* d'Orbigny (1853 : 508, pl. 722, figs. 2–5) and *D. doma* d'Orbigny (1853 : 509, pl. 722, figs. 6–10), both Lunulitidae from the Senonian of France. Canu (1900 : 378) indicated the type species of *Discoflustrellaria* to be *D. clypeiformis*, yet Canu & Bassler (1929*b* : 479) seem to have regarded *D. dactylus* as the type species when they stated, " D'Orbigny's name *Discoflustrellaria* is the older, but the French author did not give a single figure of the genotype. The latter was figured only in 1908 by Canu." This is presumably a reference to Canu (1908 : 103, pl. 9, fig. 18) who described and illustrated *D. dactylus* which Canu & Bassler (1929*b* : 478) referred to *Kionidella*. Thus Canu & Bassler seem to have been mistaken in considering *Kionidella* a synonym of *Discoflustrellaria*.

Kionidella hastingsae[13] sp. nov.

(Text-figs. 78, 79)

HOLOTYPE. D.48971 (Text-fig. 78).

PARATYPE. D.48972 (Text-fig. 79).

DIAGNOSIS. *Kionidella* with zooecia wide and rhombic in frontal aspect, the frontal wall finely pitted ; oral condyles slightly proximal to mid-length, and sinus as broad as distal part of orifice ; avicularia paired, lateral, relatively small, and with pivotal bar ; rostrum rounded ; ovicells large, pitted, the fertile zooecia with widened orifice.

DESCRIPTION. *Zoarium* cylindrical, tubular, composed of a single layer of zooecia ; ancestrular end not preserved ; axial hollow circular in cross section, slightly larger in diameter than a zooecium. Zooecia in 14 very regular longitudinal rows round surface of cylinder.

Zooecia vase-shaped, their long axes perpendicular to zoarial axis, with only orifices and small part of frontal wall, of rhombic shape, exposed at outer surface. Frontal surfaces of adjoining zooecia separated by distinct grooves. Frontal wall imperforate, convex, finely pitted. Interzooecial communication by a few simple pores placed near base of distal and lateral walls.

Orifice elliptical, longer than wide, divided just proximal to middle by a pair of small, lateral, proximally inclined condyles, the sinus thus formed being as broad as the distal part of the orifice.

Avicularia adventitious, usually paired, placed in lateral corners of frontal surface just distal to middle of orifice. Avicularian opesia sub-circular, divided by a pivotal bar. Rostrum rounded, but somewhat elongated, directed inwards and slightly distally over orifice.

Ovicell hyperstomial, convex but not much raised above zoarial surface, semicircular, of about same length as zooecium. Surface finely pitted, imperforate. Orifice of fertile zooecia widened.

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[13] After Dr. Anna B. Hastings.

MEASUREMENTS :

Ordinary zooecia

Lz (5) 0·349 (0·0693) mm., 0·26–0·44 mm.
lz (5) 0·383 (0·0237) mm., 0·34–0·39 mm.
ho (5) 0·157 (0·0097) mm., 0·14–0·17 mm.
lo (6) 0·117 (0·0100) mm., 0·10–0·13 mm.
Lav (6) 0·141 (0·0200) mm., 0·13–0·17 mm.

Ovicelled zooecia

lo (4) 0·180 (0·0070) mm., 0·17–0·19 mm.
Lov (5) 0·209 (0·0215) mm., 0·17–0·22 mm.

REMARKS. This species is most like *K. obliqueseriata* Koschinsky (1885 : 69, pl. 7, figs. 13*a*, *b*) from the Lutetian of Bavaria. The two species differ primarily in the form of the avicularium : in *K. obliqueseriata* it is single and has a long, pointed rostrum. *K. excelsa* Koschinsky and *K. dactylus* (d'Orbigny) differ from *K. hastingsae* in the form of the avicularium and also in the shape of the zooecia and orifice.

Family **ORBITULIPORIDAE** Canu & Bassler

Genus ***ORBITULIPORA*** Stoliczka

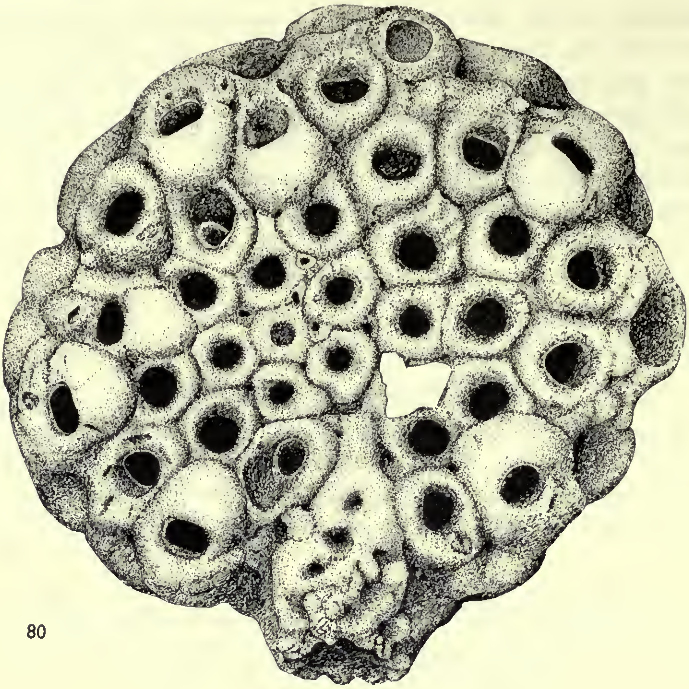
Orbitulipora petiolus (Lonsdale)

(Text-fig. 80)

1850 *Cellepora petiolus* Lonsdale : 151.
1854 *Cellepora petiolus* Lonsdale ; Morris : 120.
1862 *Orbitulipora haidingeri* Stoliczka : 91, pl. 3, fig. 5.
1867 *Orbitulipora petiolus* (Lonsdale) Reuss : 217, pl. 1, figs. 1, 2.
1881 *Orbitulipora petiolus* (Lonsdale) ; Mourlon : 180, 191, 202.
1889 *Orbitulipora petiolus* (Lonsdale) ; Vine : 163, pl. 5, fig. 10.
1893 *Biselenaria offa* Gregory : 235, pl. 30, figs. 4, 4*a* (not fig. 5).
1893 *Orbitulipora petiolus* (Lonsdale) ; Gregory : 253, pl. 31, figs. 12–14.
1907*b* *Orbitulipora petiolus* (Lonsdale) ; Canu : 102.
1919 *Orbitulipora petiolus* (Lonsdale) ; Waters : 91.
1926 *Orbitulipora petiolus* (Lonsdale) ; Canu : 758, pl. 30, fig. 5.
1929*a* *Orbitulipora petiolus* (Lonsdale) ; Canu & Bassler : 49.
1929*b* *Orbitulipora petiolus* (Lonsdale) ; Davis : 111.
1931 *Orbitulipora petiolus* (Lonsdale) ; Canu & Bassler : 16, pl. 3, figs. 1–22 ; pl. 4, figs. 1–4.
1933 *Orbitulipora petiolus* (Lonsdale) ; Dartevelle : 108.
1936 *Orbitulipora petiolus* (Lonsdale) ; Dartevelle : 29.
1939 *Orbitulipora petiolus* (Lonsdale) ; Franke : 64, pl. 3, figs. 2*a*–*d*.
1963 *Orbitulipora petiolus* (Lonsdale) ; Malecki : 137, pl. 15, fig. 5.

FIGURED SPECIMEN. D.48973 (Text-fig. 80).

ADDITIONAL MATERIAL. One hundred and forty-eight specimens, D.48974–D.49073.



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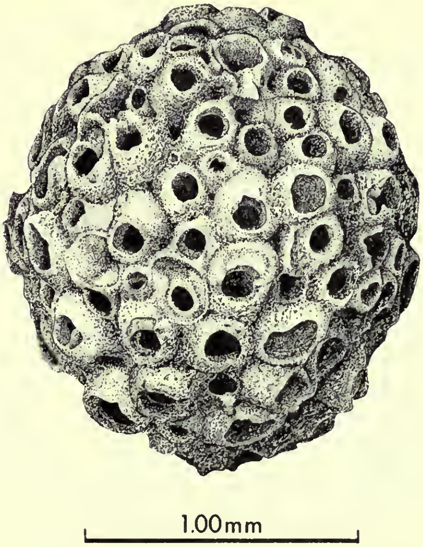

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FIGS. 80–81. Fig. 80. *Orbitulipora petiolus* (Lonsdale). D.48973. Lateral view of discoidal zoarium showing well-developed basal peduncle and several ovicelled peripheral zooecia. Fig. 81. *Batopora glandiformis* (Gregory). D.49074. Lateral view of globular zoarium. Three ovicelled zooecia and three vicarious avicularia are visible.

Diagnosis. *Orbitulipora* with discoidal zoarium circular in lateral outline but for the basal peduncle.

Description. *Zoarium* discoidal, flat on both sides, circular in lateral outline save for the basal peduncle. Zooecia arranged in two laminae, their basal walls in contact, those of each lamina in approximate annular arrangement, the largest zooecia at the periphery, the smallest at the centre of the face. Distal margins of zooecia directed towards centre of face. The central zooecia are often covered by randomly oriented, superposed zooecia. Peduncle equal to about four zooecia in size, the exterior irregularly wrinkled and pitted, the interior smooth and hollow, extending nearly to centre of zoarium.

Zooecia irregularly rhombic, pentagonal, or hexagonal, separated by deep grooves. Frontal wall moderately thick, smooth or finely granular, slightly convex, without pores or areolae.

Orifice central, taking up almost the whole frontal surface of zooecium, subcircular, unmodified but buried in thick peristome.

Ovicell hyperstomial, globular, smooth, with distinct distal rim. Orifice of fertile zooecia slightly wider than that of ordinary zooecia. Ovicells developed on zooecia of outer few annulae, on the sides towards the centre of the zoarial face, or on superposed zooecia nearer the centre of the face.

Heterozooecia unknown.

Measurements:

Zoarium

Zoarial height (5) 2·072 (0·5977) mm., 1·26–2·87 mm.
Length of peduncle (5) 0·333 (0·1071) mm., 0·17–0·44 mm.

Ordinary zooecia (at periphery)

Lz	(10)	0·345	(0·0380) mm.,	0·27–0·38 mm.
lz	(10)	0·322	(0·0421) mm.,	0·24–0·38 mm.
ho	(10)	0·132	(0·0259) mm.,	0·09–0·16 mm.
lo	(10)	0·153	(0·0142) mm.,	0·13–0·17 mm.

Ovicelled zooecia

Lov	(6)	0·252	(0·0280) mm.,	0·24–0·31 mm.
lo	(6)	0·185	(0·0476) mm.,	0·17–0·21 mm.

Remarks. In their detailed study of this species, Canu & Bassler (1931 : 16–22) assumed that the centre of the disc-shaped zoarial frond is the ancestrular region, the actual ancestrula lying at the top of the peduncular tube covered by superposed zooecia. The ovicells of the Upper Bracklesham specimens are typical hyperstomial ones, not recumbent as Canu & Bassler (1931 : 17) described them. Avicularia and vibracula are lacking in the Upper Bracklesham specimens ; the structures illustrated by Canu & Bassler as avicularia (1931 : pl. 3, fig. 15) and vibracula (1931 : pl. 3, fig. 21) might be broken ovicells.

As mentioned above (Morphology section, Zoarial Characters), Canu (1931 : 144–147) and Canu & Bassler (1931 : 19–21) supposed *Orbitulipora* to be free-swimming ; Waters (1919 : 90) had earlier suggested the more likely explanation of the peduncle of *Orbitulipora* as a structure for attachment to the substrate.

Silén (1947 : 33) noted that the reversal of the normal proximal-distal relationship in the zoarium of *Orbitulipora* is similar to that in the Conescharellinidae.

DISTRIBUTION. Eocene (Auversian) ; France, England. Eocene (Auversian, Bartonian) ; Belgium. Eocene (Ludian) ; Poland, ?Italy. Oligocene (Lattorfian) ; Belgium, Germany.

Genus ***BATOPORA*** Reuss

1867 *Batopora* Reuss : 223.
1929*a* *Atactopora* Canu & Bassler : 51, *non* Morren.
1931 *Atactoporidra* Canu & Bassler : 22.

TYPE SPECIES (chosen by Waters 1919). *Batopora stoliczkai* Reuss 1867 : 223, pl. 2, figs. 2–4. Oligocene (Lattorfian) ; Germany.

DIAGNOSIS. Frontal wall calcareous, granular or smooth, without pores or areolae. Orifice sub-circular to semi-circular, with nearly straight proximal margin. Condyles, sinus and ascopore lacking. Whole frontal wall built up round orifice as a kind of peristome. Zoarium spherical, ellipsoidal, discoidal, or conical ; hollow or solid ; the base with a special enlarged pore opening into an axial hollow which runs part way up the zoarium. Zooecia erect, arranged in several laminae, the superficial ones large, with or without ovicells, the deep ones small, without ovicells ; distal margins of zooecia directed apically. Ovicell hyperstomial, globular, smooth.

REMARKS. The structure of *Batopora* was studied in detail by Waters (1919) ; the two German Oligocene species, *B. stoliczkai* Reuss and *B. multiradiata* Reuss, considered to be the same by him (1919 : 83, 84), have been re-illustrated by Franke (1939 : pl. 2, figs. 3*a*, *b* ; pl. 3, figs. 1*a*, *b*) as separate species.

Canu & Bassler (1929*a* : 51) established *Atactopora*, later re-named *Atactoporidra*, for Orbituliporids having hollow cylindrical to globular zoaria, differing from *Batopora* which supposedly has conical zoaria. This difference does not seem uniform in the species referred to the two genera, and, furthermore, the type species of *Batopora* has the *Atactoporidra*-type zoarium.

Batopora glandiformis (Gregory)

(Text-fig. 81)

1893 *Heteropora glandiformis* Gregory : 261, pl. 32, fig. 11.
1934 *Atactoporidra glandiformis* (Gregory) Davis : 205.

HOLOTYPE. B.4511, Edwards Collection. Barton Beds ; Barton, Hants.

FIGURED SPECIMEN. D.49074 (Text-fig. 81).

Additional material. Twenty-six specimens, D.49075–D.49100.

Diagnosis. *Batopora* with nearly solid, usually spherical zoarium having an inconspicuous basal pit which extends only a short distance up axis ; superficial zooecia having large, semi-circular orifices and well-developed ovicells ; deep zooecia with much smaller, sub-circular orifices.

Description. *Zoarium* globular, usually spherical, sometimes ellipsoidal or almost discoidal ; apical end rounded, basal end slightly more pointed, with a central, circular pit which is inconspicuous and only slightly larger than a zooecial orifice and surrounded by a thin, raised collar. Zooecia arranged irregularly, their distal margins directed towards the apical end of the zoarium. Deep zooecia with only their small orifices showing between larger superficial zooecia.

Zooecia erect, their major axes perpendicular to zoarial surface, with only a small part of the frontal wall, surrounding the orifice, visible frontally. Superficial zooecia protuberant, irregularly polygonal, separated by deep depressions in which orifices of deep zooecia appear. Frontal wall thin, very convex, granular, without pores or areolae.

Orifice of superficial zooecia semi-circular, broadly rounded distally, slightly rounded proximally. Orifice of deep zooecia smaller and sub-circular. Peristome, spines, condyles and sinus all lacking.

Ovicell hyperstomial, small, globular, imperforate, finely granular, present on superficial zooecia only. Orifice of fertile zooecia slightly wider than that of ordinary superficial zooecia.

Avicularia rare, vicarious, about half as large as superficial zooecia, with rounded rostrum and pivotal bar.

Measurements :

Zoarium

Zoarial length (4) 1·706 (0·3086) mm., 1·32–1·96 mm.
Zoarial width (4) 1·511 (0·1812) mm., 1·28–1·71 mm.

Ordinary superficial zooecia

Lz (8) 0·245 (0·0438) mm., 0·19–0·31 mm.
lz (8) 0·239 (0·0333) mm., 0·17–0·27 mm.
ho (8) 0·105 (0·0127) mm., 0·09–0·12 mm.
lo (8) 0·105 (0·0203) mm., 0·09–0·13 mm.

Deep zooecia

ho (4) 0·083 (0·0118) mm., 0·07–0·10 mm.
lo (4) 0·073 (0·0086) mm., 0·07–0·09 mm.

Ovicelled zooecia

Lov (3) 0·125 (0·0131) mm., 0·11–0·14 mm.
lo (3) 0·120 (0·0086) mm., 0·11–0·13 mm.

Avicularia

Lav (2) 0·128 (0·0000) mm., 0·13 mm.

REMARKS. Gregory's (1893) erroneous placing of this species in the Cyclostome genus *Heteropora* was first noted by Waters (1919 : 92) who considered the species a young stage of *Orbitulipora petiolus*. Davis (1934 : 205) recognized the true affinities of the species.

DISTRIBUTION. Eocene (Bartonian) ; England.

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MIOCENE RHINOCEROSES OF EAST AFRICA

D. A. HOOIJER

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 13 No. 2
LONDON: 1966

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MIOCENE RHINOCEROSES OF EAST AFRICA

BY

DIRK ALBERT HOOIJER D.Sc.

Rijksmuseum van Natuurlijke Historie, Leiden

Pp. 117–190 ; 15 *Plates*

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FOSSIL MAMMALS OF AFRICA No. 21

MIOCENE RHINOCEROSES OF EAST AFRICA

By D. A. HOOIJER

> A en juger d'après l'assurance avec laquelle certains auteurs ont attribué des noms spécifiques aux restes les plus insignifiants de Rhinocéros fossiles, on pourrait croire que la détermination des animaux de ce groupe est chose aisée. Ceux qui se sont sérieusement occupés de ce sujet savent que le contraire est vrai.
>
> H. G. STEHLIN

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SYNOPSIS

Four species of Rhinocerotidae are described from the Tertiary (Miocene) of East Africa, including a new species *Dicerorhinus leakeyi*. The bearing of these Rhinoceroses on the time placement of the Miocene East African faunas is discussed, resulting in a tentative correlation with the Burdigalian of Europe, although some of the Rusinga sites appear to be younger, later Miocene or even Pliocene.

I. INTRODUCTION AND ACKNOWLEDGMENTS

RHINOCEROSES have a reputation for being difficult animals to deal with as fossils. In spite of an enormous amount of scientific literature, the present state of our knowledge and comprehension of this group is comparable only to that of O. C. Marsh's grasp of the equids.[1] H. F. Osborn's oft-cited " Phylogeny of the rhinoceroses of Europe " (1900) has never been followed up by a monographic treatise, and the first part of his " The extinct rhinoceroses " (1898), the only part ever published, is devoted to generalities and the acerathere rhinoceroses of the White River Beds of Nebraska and the Dakotas. A comprehensive paper on the Tertiary Rhinocerotidae of Eurasia is sadly lacking and treatment of the fossil material in the scattered literature is very uneven and incomplete.

For a sound diagnosis of a new fossil species we need the whole skull, with the incisors and canines, if any (premaxillaries have often been lost). We need also the skeleton, in particular the metapodials, which are rarely found associated with a skull. These requirements, therefore, are seldom fulfilled (cf. my motto, taken from Stehlin 1925 : 106). Too much reliance has often been placed upon individually variable molar crown structures or labile cingula. New fossil species (and genera) have occasionally been based on milk teeth mistaken for permanent teeth, or on female specimens of previously described forms. Fragmentary fossil remains of rhinoceroses have more than once been described as hippopotami, and vice versa. Foot bones have been confounded with those of anthracotheres or chalicotheres. Wrong identifications, once published, have a habit of perpetuating themselves in the literature, to the detriment of a better understanding. In order to soften these pontifical remarks I hasten to add that I have not been able always to avoid these pitfalls in my own rhinoceros work either.

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[1] This sagacious comment was made by Dr. Stanley Westoll in the discussion following my paper at the Symposium of Vertebrate Palaeontology and Comparative Anatomy in Bristol on 23rd September, 1964.

In the last few decades representatives of three genera of Rhinocerotidae from the Tertiary of Eurasia have been found in Africa. These are *Dicerorhinus*, *Aceratherium* and *Brachypotherium*.

The so-called phyletic line of *Dicerorhinus* Gloger comprises a number of evidently collateral forms with slender limbs and feet ranging from the Aquitanian (Upper Oligocene) through the Pleistocene of Europe, and up into the Holocene of Asia. It seems unlikely that the fossils should all be referred to the same genus, and that this is the genus of the extant Sumatran species. *D. sumatrensis* (Fischer) is the most primitive among the five surviving species of rhinoceroses, and may truly be said to represent a Miocene stage of evolution of teeth and skeleton, but its immediate ancestry is unknown apart from what can be derived from subfossil remains found in Sumatran caves (Hooijer 1946*a*, *b*). This suggests a decrease in tooth and limb size since the formation of the cave deposits (presumably Early Holocene), which is a common phenomenon. The further use of the generic name *Dicerorhinus* for the Tertiary and Pleistocene forms, however, is to be recommended; we have far too many generic names in the Rhinocerotidae anyway (many monotypical), and it is a relief to see a case in which the generic limits are drawn as broadly as in *Dicerorhinus*. The first African representative to become known is the well-documented *Dicerorhinus primaevus* Arambourg (1959) from the Pontian (Lower Pliocene) of Wad el Hammam in Algeria; earlier records are ambiguous.

The genus *Aceratherium* Kaup, with its persistently tetradactyl fore feet, and limbs as slender as in *Dicerorhinus*, ranges from the Stampian (Middle Oligocene) up into the Pontian in Europe and Asia, showing some phylogenetic advance. It was first recorded from East Africa (Moruaret Hill near Losodok or Lothidok, Kenya) by Deraniyagala (1951) as *Turkanatherium* Deraniyagala; Arambourg's earlier record of a lower molar, an epistropheus, an astragalus, two metatarsals and some phalanges from Losodok as *Aceratherium* ? spec. might also belong to *Dicerorhinus*. The dentition of *Aceratherium acutirostratum* (Deraniyagala) has recently been described from the Miocene of the Karugamania region, Lake Albert, Western Rift Valley in Congo (Hooijer 1963).

In the short-limbed and -footed genus *Brachypotherium* Roger of Europe (Burdigalian (Lower Miocene) through Pontian), often placed in the North American genus *Teleoceras* Hatcher that may have been derived from it (Osborn 1910 : 292), there is some evolutionary progress (in the shortening of the limbs and metapodials particularly). In 1920 Fourtau recorded this genus (as *Teleoceras*) from the Burdigalian of Moghara in Egypt, and I have added a more progressive species from the Miocene of the Sinda-Mohari region, Lower Semliki, Congo (Hooijer 1963).

Thus, there are various previous records of Tertiary Rhinocerotidae from Africa (in this connexion mention should be made of the well-described but specifically unidentified last upper molar from Karungu, Kenya, recorded by Andrews 1914). Sonia Cole (1950) listed *Aceratherium* from the Miocene of Rusinga Island, Karungu, and Maboko Island, as well as *Teleoceras* from Rusingu and Karungu (Cole 1950 : 29), and also published a photograph of a rhinoceros skeleton in the process of being excavated from the Lower Hiwegi Beds in Rusinga in 1947 (1950, pl. 1). In a provisional list of the Miocene faunas of East Africa, Le Gros Clark & Leakey (1951 : 5) recorded Rhinocerotidae from the following nine sites : Karungu, Rusinga Island, Chianda Uyoma, Ombo, Maboko Island, Songhor, Losodok, Loperot and Tambach.

The collections described in the present paper, upon which the above cited locality records are based, are for the most part in the National Museum Centre for Prehistory and Palaeontology, Nairobi, Kenya, and were generously offered to me for study and report by Dr. L. S. B. Leakey in April, 1963. Much Miocene East African rhinoceros material is in the Department of Palaeontology of the British Museum (Natural History), London, and this I have been lent. Dr. W. W. Bishop of the Kampala Museum, Uganda, has sent me Miocene material from the Napak volcanics, Karamoja, Uganda, which is likewise described in the present paper.

I am very much indebted to Dr. L. S. B. Leakey for entrusting this interesting material to me, as well as to Dr. W. W. Bishop for the Napak material and to Dr. A. J. Sutcliffe for arranging to have the British Museum material made available. I am very grateful to Mrs. S. C. Coryndon, Mrs. Sonia Cole and Dr. T. Whitworth for valuable information and kind advice.

A systematic account of the genera and species of Rhinocerotidae from the East African Miocene is given in the following chapters. The specimens from the British Museum (Natural History) have numbers preceded by an M. The conventional dental nomenclature has been used and the measurements of the cheek teeth have been taken at the base of the crown, the length (ant. post.) in the upper P and M externally except in M^3, where it is taken internally. Most of the specimens, in addition to the catalogue number, bear letters indicating the sites, such as R. for Rusinga Island, Rs. for a surface find in Rusinga, followed by a sub-site number, e.g., R.1, R.2, etc. (Le Gros Clark & Leakey 1951 : 10) ; K stands for Karungu, KB or MB for Maboko (= Kiboko) Island, and S or Sgr for Songhor (Whitworth 1958 : 2). Maps showing the location of the various sites in Kenya and Uganda will be found in Whitworth (1958 : 2) and Bishop (1958), a map showing the sub-sites in Rusinga was given by Le Gros Clark & Leakey (1951 : 9). On the advice of Dr. Leakey the relationship of the sites to the fossiliferous strata in Rusinga Island has been omitted at this stage.

II. SYSTEMATIC DESCRIPTIONS

Genus ***DICERORHINUS*** Gloger 1841

Dicerorhinus leakeyi sp. nov.

(Pls. 1–3 ; Pl. 4, figs. 1, 4, 7, 8 ; Pl. 5, figs. 1–3 ; Pl. 6, figs. 7, 8, 12 ; Pl. 7, figs. 5, 6 ; Pl. 10, figs. 4, 5 ; Pl. 11 ; Pl. 13, figs. 1–5 ; Pl. 14, fig. 1 ; Pl. 15)

DIAGNOSIS. *Dicerorhinus* species with frontal and nasal horns ; upper incisors smallish, small incisors between lower canines ; inferior squamosal processes united below subaural channel. Occiput as highly elevated as in *D. sansaniensis* (Lartet). Lower border of mandible nearly straight as in *D. sansaniensis*, not curved upward in symphysial region as in *D. schleiermacheri* (Kaup), *D. orientalis* (Schlosser) and *D. ringstroemi* Arambourg. Size of skull as in *D. schleiermacheri* and *D. orientalis*, larger than in *D. sansaniensis* and smaller than in *D. ringstroemi*. Teeth intermediate in size between those of *D. schleiermacheri* and those of *D. sansaniensis*.

Upper premolars with protoloph and metaloph united internally up to at least 15 mm. from crown base, cingulum weak, protocone not markedly constricted off. Upper molars with low and wide lingual entrance to medisinus, internal cingulum very weak or absent, protocone not or hardly constricted off, antecrochet not prominent, not blocking medisinus, ectoloph depressed between the roots, crochet and crista weak or absent, M^3 bulging out at junction of ectoloph and metaloph.

The specific name is given in honour of Dr. L. S. B. Leakey, who collected the type in 1935.

HOLOTYPE. The skull and associated mandible from Rusinga (Pl. 1 ; Pl. 2, figs. 1, 2).

HORIZON AND LOCALITY. Lower Miocene ; Rusinga Island, Kenya.

DESCRIPTION. The skull and associated mandible were collected at Rusinga by Dr. L. S. B. Leakey in 1935. Both are somewhat crushed and in part restored or fortified with plaster. The crushing is mostly laterally : the two upper tooth-rows are only 30 mm. apart in the premolar region and 50 mm. between the last molars. The tooth-rows are somewhat displaced longitudinally : the right tooth-row is shifted 2 cm. backward relative to the left. The palate is broken. The whole of the post-dental basal portion of the skull is lost except for the right zygomatic arch and glenoid cavity with the postglenoid and post-tympanic processes. The zygomatic arch is pushed inward and slightly backward, reducing the width of the temporal fossa to a mere 3 cm. Of the glenoid cavity the outer portion is displaced backward ; the outer angle of this cavity is on the same transverse level as the huge postglenoid process. This distortion evidently took place while the condyle of the mandible was lodged in the cavity, for the condyle is deformed in the same way, with its outer part pushed backward, and it fits exactly into the cavity as it is. Only a small portion of the left parietal is preserved, and it is thrust upward.

When viewed from the right side, however, the fronto-parietal surface is relatively well preserved, rising backward and upward from the orbit in a gentle curve which seems unaffected by distortion. The top of the occiput has broken off. The right fronto-parietal crest is preserved, and evidently did not meet its fellow on the other side of the skull, the least distance between the crests being approximately 3 cm. The temporal crest is for the most part preserved, but undamaged only in its lower portion. Below the external auditory meatus the two inferior squamosal processes are seen to be firmly united.

On the ventral surface of the skull nothing remains behind the last molars but the base of the pterygoid process on the left side. The hinder margin of the palate is on a level with the front of M^2.

The frontal region of the skull is only superficially damaged, and it is clear that there is a median boss just above the anterior border of the orbit, indicating the presence of a frontal horn. The postorbital processes of the frontals are damaged, and the width of the skull at this point cannot be determined. The anterior border of the orbit is above the anterior border of M^2. The nasal bones are well preserved on both sides, although laterally compressed, and are convex and rugose above, pointing to the presence of a nasal horn. The tips of the nasals are slightly bent downward. The naso-maxillary notch is well shown on either side, extending backward to above the anterior border of the first tooth, the well-worn DM^1. The depth of the notch is 16 cm. from the nasal tips on the left, and 18 cm. from the tips on the right side. Only 25 mm. behind it there is the infraorbital foramen, placed above P^2.

The premaxillaries are fortunately preserved in the skull, forming two strong, 4 cm. high, converging bones that are slightly inclined downward. They each carry a relatively small incisor, but no other teeth behind these. The premaxillary-maxillary suture is obliterated, but together with the maxillary processes to which they are attached the premaxillaries have a length of 14 cm., projecting only slightly less forward than the nasals. The height from the lower surface of the tips of the premaxillaries to the tips of the nasals is 11 cm.; the height of the skull from the alveolar margin of M^1 to the upper surface of the frontals is approximately 16 cm.

The mandible belonging to the skull is well preserved on the right side; the left body is broken off behind M_3. The high ascending portion with the coronoid and condyloid processes fits well into the laterally compressed temporal fossa, and the distorted condyle articulates in the glenoid cavity when the tooth-rows are in occlusion. The lower canines are close to their antagonists, the upper incisors. Between the canines the mandible shows two small incisors. The profile of the mandible is nearly straight ventrally, with the symphysial portion only slightly curved upward, and the angular process is broad and well rounded behind.

The characters of the present skull and mandible, notably the indications of the presence of a nasal and of a frontal horn, the presence of smallish upper incisors, the small incisors between the lower canines and the union of the two inferior squamosal processes, leave no doubt as to their belonging to the genus *Dicerorhinus*. To this genus a number of Tertiary and Pleistocene species have been referred, evidently forming several collateral lines, in Europe as well as in Asia, where it survives as the Sumatran rhinoceros, *Dicerorhinus sumatrensis* (Fischer). The extant form is not the most advanced: although it lacks the central lower incisors present in the fossil forms it has an opening between the postglenoid and the post-tympanic process, a supposedly less specialized character than the union of these seen in fossil *Dicerorhinus* (see Flower 1876 : 456).

A second individual of *Dicerorhinus leakeyi* from Rusinga is represented by an upper dentition and right zygomatic arch, and a mandible of which only the right half is entirely preserved. These specimens are marked no. 2, R.1, 1947. The upper dentition agrees perfectly with that of the holotype skull of *D. leakeyi* in characters, and the lower jaw differs only in being slightly convex anteroposteriorly below, longer, less high below M_3, and in the absence of P_1 (Pl. 2, figs. 3–4).

Measurements of the holotype skull and mandible of *D. leakeyi* as well as of the lower jaw no. 2 from Rusinga are given in Table 1 together with those of *Dicerorhinus sansaniensis* (Lartet) from the Vindobonian of Sansan (Kaup 1854 : 3 ; Filhol 1891 : 200), *Dicerorhinus schleiermacheri* (Kaup) from the Pontian of Eppelsheim (Kaup 1834 : 40–41), *Dicerorhinus orientalis* (Schlosser) from the Pontian of Pikermi (Gaudry 1862–67 : 184, as *Rh. pachygnathus*, and p. 206, as *Rh. schleiermacheri* ; see Ringström 1924 : 12), and *Dicerorhinus ringstroemi* Arambourg (1959 : 73) from the Pontian of North China (Ringström 1924 : 12, as *D. orientalis*). Table 1 shows that the Rusinga form is rather similar in size to *D. schleiermacheri* and *D. orientalis*, *D. sansaniensis* being smaller, and the Chinese species larger.

TABLE 1

Measurements of skull and mandible of *Dicerorhinus* (mm.)

	D. leakeyi		*D. sansaniensis*	*D. schleiermacheri*	*D. orientalis*	*D. ringstroemi*
	Type	no. 2				
Length from occipital crest to tip of nasal bones	*c.* 630	—	468	640	645	745
Width over postorbital processes	—	—	—	200	—	236
Height of occiput from basion	—	—	—	200	210	220
Depth of naso-maxillary notch from tip of premaxillaries	*c.* 145	—	—	142	—	—
From naso-maxillary notch to anterior border of orbit	*c.* 135	—	95	160	150	—
From anterior border of orbit to external auditory meatus	260	—	218	246	—	—
From tip of premaxillaries to anterior border of P^2	150	—	—	154	—	—
Length of mandible from front to back of angular process	500	530	470	510	*c.* 500	635
Length from front to P_2	110	90	—	—	90	*c.* 95
Length of symphysis	130	120	115	142	—	132
Height below M_3	105	85	70	—	90	115
Height of coronoid process	*c.* 275	270	—	278	—	—
Height of condyloid process	230	220	192	248	—	—

The *Dicerorhinus* skull from Rusinga differs from that of *D. schleiermacheri* as figured by Kaup (1834, pl.10, fig. 1 ; 1854, pl. 10, fig. 1) in the occiput being more elevated ; the fronto-parietal profile is more concave. There is a marked sagittal crest in *D. schleiermacheri*, and the premaxillaries are not inclined downward as in the Rusinga skull but project straight forward. The symphysial portion of the mandible is much more curved upward in *D. schleiermacheri* than in *D. leakeyi* so that the upper I and the lower C nearly touch each other just the same. The infraorbital foramen is placed further back in *D. schleiermacheri* than in *D. leakeyi*, viz., *c.* 40 mm. behind the naso-maxillary notch and above P^3. The lower border of the mandible is not straight, but slightly concave behind the symphysis in *D. schleiermacheri* ; the angular process, however, is equally rounded.

The almost equally large skull of *D. orientalis* from Pikermi (Gaudry 1862–67 : pl. 32, fig. 1, as *Rh. schleiermacheri*) likewise has the occiput less elevated than the Rusinga skull, but it does not have a sagittal crest. The premaxillaries are incomplete and carried either reduced incisors or none at all (Ringström 1924 : 18–20). The infraorbital foramen is nearer to the naso-maxillary notch (12–18 mm.) and is placed above P^3. The mandible of *D. orientalis* (Gaudry 1862–67 : pl. 28, fig. 1, as *Rh. pachygnathus* but referred to *orientalis* by Ringström 1924 : 21) has a slightly convex lower margin ; the angular portion is incomplete, but the lower canines are quite reduced.

The skull of *D. ringstroemi* from China (Ringström 1924 : 6, text-figs. 1, 2) again does have the flat profile of *D. schleiermacheri* and *D. orientalis* ; the fronto-parietal crests do not meet and form no sagittal crest (least distance 45 mm.). The maxillary processes and the premaxillaries have broken off. The mandible (Ringström 1924 : 10, text-figs. 3, 4) has a slightly convex lower profile and quite reduced canines, as in *D. orientalis* ; the symphysis is curved upward.

It is only in the skull and mandible of *D. sansaniensis* (Duvernoy 1853 : pl. 1, fig. 1*a* ; Kaup 1854 : pl. 10, fig. 2 ; Filhol 1891, pls. 13, 14) that the salient characters of *D. leakeyi* are present. The occiput is raised to the same extent as in the Rusinga skull, and the mandible is not much curved upward in its symphysial portion and nearly straight below in profile. Unfortunately the premaxillaries are missing in the Sansan skull, but the lower C are present. They are relatively well developed and between them there are two small incisors.

Unfortunately the available skull of *Dicerorhinus primaevus* Arambourg (1959) from the Pontian of Wad el Hammam in Algeria is that of a young individual with milk teeth, and M^1 erupting, lacking the posterior portion and the premaxillaries. The skull of *Dicerorhinus caucasicus* Borissiak (1938) from the Vindobonian Chokrak beds in North Caucasus is deformed and incompletely known. Hence, only the dentition and skeleton of these forms are available for comparison.

Regarding the dentition of *Dicerorhinus leakeyi*, it is most convenient to deal with all the dental material in the East African Miocene collection that may be safely referred to *Dicerorhinus*.

Both upper incisors are preserved in the holotype skull of *D. leakeyi* and of the upper dentition no. 2, R.1 (Pl. 4, fig. 7). The crowns are elongated anteroposteriorly, with the lateral surface convex and the medial undulating, convex in front and behind and depressed in between. The lateral surface is more worn down than the medial.

The root is transversely compressed, diminishing slightly in diameters toward its blunt apex.

There are no less than eight isolated upper incisors agreeing well in shape and size with those of *D. leakeyi*, three of which are in the British Museum (Natural History) : a left specimen marked Rs.3, Rusinga, a right specimen marked R.1, Rusinga, and a left specimen marked R.11, Rusinga. The National Museum specimens consist of four from the right side : no. 109, 1949, West side of Hiwegi, Rusinga (Pl. 4, fig. 8), no. 275, 1949, Kathwanga, Rusinga, no. 81, 1950, R.1–1a, Rusinga, and F.3056, Kathwanga, Rusinga, and a left specimen numbered F.3060, Rusinga. Measurements are given in Table 2.

Table 2

Measurements of upper incisors of *Dicerorhinus leakeyi* (mm.)

	Type		no. 2						
	dext.	sin.	dext.	sin.	Rs.3	R.1	R.11	no. 109	no. 275
Ant. post.	38	37	35	34	36	33	—	34	—
Transv.	18	18	16	15	14	15	14	15	15

	no. 81	F.3056	F.3060
Ant. post.	—	32	32
Transv.	14	15	—

The root is well preserved in most specimens, varying from 3·5 to 4 cm. in length. The amount of individual variation within this series is not very great. A very much larger upper incisor from Rusinga will be dealt with below under *Brachypotherium*.

The upper incisors of *D. schleiermacheri* (Kaup 1834 : 34, pl. 11, figs. 3, 4) are similar in crown size to those of *D. leakeyi* : diameters 35 by 16 mm. and 33 by 13 mm., but the root appears to be more massive in the Eppelsheim species. Moreover, there is a small second incisor behind the larger one in each premaxillary, 8 mm. in diameter (Kaup 1834 : 34) ; of these there is no trace in the Rusinga skull. In *D. orientalis* the upper incisors have not been found, and from the tapering (incomplete) premaxillaries it may be concluded that they were either reduced or absent. The same applies to *D. ringstroemi*.

The foremost teeth present in the holotype skull *D. leakeyi* are the first upper milk molars, DM^1. They are, however, too worn and damaged to reveal much of their structure ; the milk dentition of *Dicerorhinus* will be dealt with later.

The upper premolars P$^{2-4}$ of the type skull of *D. leakeyi* as well as those of the dentition no. 2, R.1 (Pl. 2, fig. 3, Pl. 5, figs. 2, 3), (P^2 sin. is not preserved) are much worn down. The external surface of the left P^2 and P^4 as well as that of the right P^3 in the type skull are incomplete, and the right P^2 and P^3 are incomplete internally. P^2 is worn to such a degree that a small portion of the medisinus only remains on the occlusal surface. P^3 and P^4 both have protoloph and metaloph connected internally forming a high lingual wall up to at least 12 mm. (P^3) or 15 mm. (P^4) above the enamel base; the teeth are worn down to this level. There is a weak cingulum on the internal surface, 8 mm. high on the protoloph, and slowly rising behind. In the least worn premolar (P^4) the lingual third of the medisinus, well cut off from the internal wall, and the postsinus are shown on the worn surface. The internal surface of the crowns of P^3 and P^4 has a weak vertical depression at the junction of protoloph and metaloph; the protocone is only weakly constricted off.

There are various isolated upper premolars, all much worn, that should be referred to *Dicerorhinus*, viz.,

No. 752, 1951, Rusinga, P^2 sin., incomplete postero-internally,

No. 1385, 1951, Rusinga, P^3 dext. (Pl. 6, fig. 12),

No. 2549, 1952, Rusinga, P^3 sin., damaged behind, and

No. 80, 1950, R. 1–1a, Rusinga, P^4 dext.

These specimens all have the high internal wall of the *Dicerorhinus* type; the internal cingulum is hardly visible in some specimens. Measurements have been entered in Table 3.

TABLE 3

Measurements of upper premolars of *Dicerorhinus leakeyi* (mm.)

	Type	no. 2	no. 752	
P^2, ant. post.	26	31	29	
ant. transv.	34	35	35	
post. transv.	36	37	—	
			no. 1385	no. 2549
P^3, ant. post.	29	33	31	—
ant. transv.	43	46	46	47
post. transv.	44	—	43	—
			no. 80	
P^4, ant. post.	31	38	34	
ant. transv.	51	50	52	
post. transv.	49	47	49	

The upper molars of the holotype skull of *Dicerorhinus leakeyi* are characterized by their low and wide lingual medisinus entrances. All except M^2 dext. lack portions of the external surface, while M^1 dext. is incomplete antero-internally as well. The molars of the upper dentition no. 2, R. 1, Rusinga (only those from the right side are preserved), are very similar to those of the holotype and worn to a slightly less degree; the M^2 is incomplete antero-externally and M^3 is incomplete behind. There is no manifestation of a lingual cingulum in the molars except for a small tubercle at the medisinus entrance of the M^1 in no. 2. The medisinus is not blocked by the antecrochet, which is hardly visible; the protocone is not or hardly constricted. The crochet is weak and there is no crista. The ectoloph is much depressed between the roots.

The M^3 has a character that lends it a primitive look, viz., the bulging out of the outer surface at the junction of ectoloph and metaloph. This bulge, representing the metacone and supported by a heavy postero-external root, gives the crown a trapezoid, somewhat M^{1-2}-like outline quite different from the nearly triangular outline found in the M^3 of *Aceratherium acutirostratum* (Deraniyagala) (Hooijer 1963, pl. 7, fig. 1), in which ectoloph and metaloph are confluent without a bulge to mark their junction. In this character the M^3 of *Dicerorhinus* is definitely more primitive than that of *Aceratherium.*

The projection of the metastyle and posterior half of the metacone in M^3 is lost early in the history of the Rhinocerotidae, as fully discussed by Wood (1927). In the Eocene *Hyrachyus* (Wood 1934, pl. 22) there is a marked posterior projection of the metacone and metastyle in M^3. This projection is no longer discrete in *Dicerorhinus*, having merged into the outer surface, but the basal bulge is still there.[1]

It is interesting to note that in Recent *Dicerorhinus sumatrensis* M^3 shows the same development : ectoloph and metaloph, although confluent, form a wide angle with a basal bulge (Hooijer 1946*a*, pl. 2, fig. 8, pl. 3, fig. 1).

There are numerous isolated upper molars in the East African Miocene collection that present the *Dicerorhinus* type, as follows :

No. 1163, 1950, R.1, Rusinga, M^1 sin., ectoloph incomplete,
No. 1161, 1950, R.1, Rusinga, M^2 sin. (Pl. 6, fig. 7),
No. 82, 1950, R.1–1a, Rusinga, M^1 sin. without parastyle and metastyle,
No. 37, 1947, Songhor, anterior outer fragment of left upper molar,
No. 485, 1948, Kathwanga, Rusinga, M^3 dext., outer and anterior parts lost,
No. 14, 1949, R.1, Rusinga, M^3 dext.,
No. 711, 1949, Gumba, Rusinga, M^3 dext., much worn, outer surface broken off,
two unnumbered portions of M^3 sin., Rusinga, one much worn down and with the enamel incomplete anteriorly, the other the posterior portion only,
No. 1162, 1950, R.1, Rusinga, M^3 sin., corroded enamel and incomplete behind.

The following specimens are in the British Museum (Natural History) :

M^1 dext., R.1, Rusinga, lacking metastyle,
M^2 dext., R.2, Rusinga, metastyle and part of protoloph wanting,
M^2 sin., Rusinga, lacking outer portion,
M^3 sin., R.1, Rusinga (Pl. 7, figs. 5, 6) and
M^3 dext., Rs.108, Rusinga, lacking posterior portion, weak crista.

Measurements of these specimens are presented in Table 4.

In a collection from Napak, Karamoja, Uganda, entrusted to me by Dr. W. W. Bishop, there is the anterior surface of the protoloph of a left upper molar (no. 509, Napak VI, 1961 (1)) with a very weak protocone fold that I have no doubt should be referred to *Dicerorhinus*. It can be exactly duplicated in the Rusinga material listed above.

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[1] Recently Wood (1963) described a primitive true rhinoceros from the Late Eocene of Mongolia as *Pappaceras confluens*, the specific name referring to the essentially confluent ectoloph and metaloph of M^3, a rather advanced structure in such an early Tertiary form.

TABLE 4

Measurements of upper molars of *Dicerorhinus leakeyi* (mm.)

	Type	no. 2	no. 1163	no. 82	R.1			
M^1, ant. post.	36	41	—	—	40			
ant. transv.	50	52	52	53	50			
post. transv.	46	49	49	49	47			
p. tr. : a. tr.	0·92	0·94	0·94	0·93	0·94			
			no. 1161	R.2				
M^2, ant. post.	41	43	42	43				
ant. transv.	55	55	54	55				
post. transv.	46	47	48	49				
p. tr. : a. tr.	0·84	0·85	0·89	0·89				
			no. 14	no. 711	no. 1162	R.1	Rs. 108	Rs.
M^3, ant. post.	42	46	44	45	—	42	—	43
ant. transv.	51	53	51	—	*c.* 50	50	50	54
l. outer surface	52	—	55	—	—	53	—	57

The ratio of the postero-transverse to the antero-transverse diameter shows that M^2 is relatively narrower behind than is M^1. In M^3 the metacone bulge can be seen in most specimens ; the M^3 sin. from R. 1 is entire behind and shows the bulge very well. In Recent *D. sumatrensis* the bulge is as marked : in an M^3 sin. from a Sumatran cave (Dubois Collection no. 910a) as in nearly all the Sumatran cave teeth, the roots have been eaten away by porcupines and only the enamel of the crown, nibbled at the edge, remains, but in basal view the trapezoid outline of the crown is well seen, corresponding with that made by the heavy rounded root of the metacone in the Rusinga tooth. The posterior width (metacone-hypocone) happens to be the same in the two specimens (37 mm.), and the antero-transverse diameter is also the same in the two (50 mm.). The posterior cingulum is somewhat better developed in the Rusinga specimen than in that from Sumatra, but this is a highly variable feature : in another Sumatran M^3 (Dubois Collection no. 663a) the posterior cingulum is as well developed as that in the Rusinga M^3.

The upper premolars and molars of *Dicerorhinus schleiermacheri* as figured by Kaup (1834, pl. 11, fig. 5) are larger than those in the Rusinga *Dicerorhinus* ; the length P^2–M^3 is 250 mm. as figured by Kaup against 205 mm. in the holotype skull and 220 mm. in dentition no. 2 of *D. leakeyi*. The maximal transverse diameters given in the text (Kaup 1834 : 37) are : P^4 60 mm. ; M^1 62 mm. ; M^2 65 mm., whereas in *D. leakeyi* the antero-transverse diameters are at most 52 mm. in P^4, 53 mm. in M^1 and 55 mm. in M^2. In structure, however, the Eppelsheim premolars and molars resemble those of Rusinga very closely : there is a weak internal cingulum in the premolars above which protoloph and metaloph are confluent, the protocone is weakly constricted, while in the molars the internal cingulum is absent, the medisinus entrance low and wide, the protocone constriction weak, and M^3 has a bulge at the metacone base. The crista and the crochet are weak or absent in *D. leakeyi* but these projections into the medisinus recede towards the base and hence show better in less worn teeth such as those of *D. schleiermacheri* (in various molars of *D. leakeyi* there are traces of crista and crochet). The upper dentition of *Dicerorhinus sansaniensis* (Filhol 1891 : 201, pl. 14, fig. 6 ; Pavlow 1892, pl. 5, fig. 15) agrees in characters with that of *schleiermacheri* and *leakeyi* (it shows no crista and a weak crochet), but in size it is less than that of the Rusinga *Dicerorhinus* (length P^2–M^3 190 mm., maximal width of P^4 45 mm., of M^1 46 mm., and of M^2 47 mm.). Hence, the upper teeth of *D. leakeyi* are intermediate in size between those of *D. schleiermacheri* and *D. sansaniensis*. The upper molars available of *D. primaevus* show this to be a larger species than *D. leakeyi* : the width of M^1 is 57·5 mm. and that of M^2 62·5 mm. (Arambourg 1959 : 59). In *D. caucasicus* the upper premolars as described by Borissiak (1938 : 9–13) have the crests internally confluent upon wear, as in *D. schleiermacheri*, *D. sansaniensis* and *D. leakeyi*, but in size *D. caucasicus* is nearly as small as *D. sansaniensis* (width of P^4 37 mm., of M^1 51 mm., of M^2 48 mm.).

The canines in the mandible of the holotype of *D. leakeyi* are subtriangular in cross-section, with rounded upper and lower outer edges and a sharp edge internally. At the base of the crown the diameters are 30 mm. horizontally and 21 mm. vertically. The distance between them amounts only to 11 mm., but between them, or rather crowded out below the inner edges of the canines there are two small incisors, round in section and with pea-shaped crowns 8 mm. in diameter. In mandible no. 2 there are only the alveoli of the incisors and canines, but they resemble those in the holotype very closely. The depth of the alveolus of the left canine, exposed laterally, is just over 10 cm. An isolated pair of lower canines thought to belong to no. 2 (Pl. 4, figs. 4, 5) have crowns agreeing exactly in shape and size with those of the type ; the crown length is 4·5 cm. and the roots, which are straight and gradually taper toward the apex, have a length of 9 cm.

The tip of a left lower canine, no. 980, 1950, Kiangata, Rusinga, is 30 mm. transversely at crown base and very nearly round in section at the root (30 mm. horizontally and 28 mm. vertically). The length of the worn crown is only 27 mm., indicating perhaps that it was less procumbent than the others. Whether this canine belongs to *Dicerorhinus* or to some other genus is uncertain. We have further the lower canines of the *Aceratherium* specimen described under that head.

The lower incisors and canines of *D. schleiermacheri* are similar in size to those of *D. leakeyi* ; the diameter of the incisor alveoli is 8 mm., and those of the canine 30 mm. horizontally and 22 mm. vertically (Kaup 1834, pl. 11, fig. 8 ; there is a cast in the British Museum (Natural History), no. M.2782). In the mandible of *D. sansaniensis* there are likewise small incisors between the canines (see Filhol 1891 : 201, pl. 14, fig. 1 ; Roger 1900 : 51, pl. 1, fig. 2), diameters 6 mm., and 20 mm., respectively, smaller than in the Rusinga mandibles. In *D. orientalis* as well as in *D. ringstroemi* the lower incisors or canines are much reduced (Ringström 1924, text-figs. 14, 15 and 3, 4). In *D. primaevus* only traces of the alveoli of lower incisors have been found (Arambourg 1959 : 60), and in *D. caucasicus*, as in *D. schleiermacheri* to which it may be ancestral, there are subtriangular lower canines (erupting) and two small cylindrical incisors in between (Borissiak 1938 : 16, pl. 1, fig. 4).

The lower canine described from the Miocene of the Sinda-Mohari region, Congo

(Semliki no. 527, Hooijer 1963 : 48), as possibly belonging to *Dicerorhinus* is similar to that of *D. leakeyi* although smaller (basal crown diameters 22 by 11 mm.).

All the lower premolars and molars of the holotype of *D. leakeyi* are present, including a small and slightly worn P_1. Those of dentition no. 2, R.1, 1947, are slightly larger; only the right side of the mandible is intact and it shows no trace of a P_1, while nothing is preserved of the left ramus except the isolated P_4, M_2 (Pl. 6, fig. 8) and M_3. These teeth are characterized by having a deep vertical groove externally between the two lophids, the metalophid in front and the hypolophid behind, and by the absence of an external cingulum. There are a few more mandibles presenting the same characters, as follows:

M.18921 is a mandible from Rusinga that has alveoli for the I and C as in the *Dicerorhinus* specimens. The teeth preserved are the right P_4 and M_{2-3}, and the left P_3–M_3. The ascending portions of the rami are restored with plaster behind. The teeth present no differences from those in the holotype and no.2.

No. 231, 1949, a right mandibular ramus from R.2–4, Rusinga, has P_4 and M_{2-3} *in situ*. The symphysial portion is missing, and of the postdental portion only the angular process is preserved. The teeth agree with those of *Dicerorhinus* in size and characters.

Measurements are given in Table 5.

The length of the mandibular tooth-row P_2–M_3 is 250 mm. in *D. schleiermacheri* and 196 mm. in *D. sansaniensis* (Kaup 1854 : 3), longer, and shorter, respectively,

TABLE 5

Measurements of lower premolars and molars of *Dicerorhinus leakeyi* (mm.).

	Type	no. 2	M.18921	no. 231
P_1, ant. post.	18	—	—	—
transv.	11	—	—	—
P_2, ant. post.	26	28	—	—
ant. transv.	16	16	—	—
post. transv.	17	18	—	—
P_3, ant. post.	31	34	—	—
ant. transv.	21	20	21	—
post. transv.	23	23	24	—
P_4, ant. post.	35	37	35	36
ant. transv.	26	26	26	—
post. transv.	28	28	27	—
M_1, ant. post.	—	41	—	—
ant. transv.	29	28	—	—
post. transv.	30	31	—	—
M_2, ant. post.	41	45	45	43
ant. transv.	32	30	31	—
post. transv.	31	31	31	27
M_3, ant. post.	44	51	49	44
ant. transv.	30	30	31	28
post. transv.	28	29	27	28
Length P_2–M_3	215	235	—	225

than in the *D. leakeyi* specimens (Table 5). In the figured mandible of *D. schleiermacheri* the anterior premolar P_1 is absent, but it occurs in one out of twenty-four mandibles (Kaup 1834 : 37, see pl. 11, fig. 8*a*), and it is about 11 by 7 mm. in crown diameters. In *D. sansaniensis* a P_1 is present in the figured mandible, diameters 15 by 10 mm. (Filhol 1891 : 201). In the second mandible of *D. leakeyi* P_1 has not developed. It is evident that the presence or absence of this tooth is not a character of great significance.

Apart from a few isolated lower molars that have a flattened external surface and therefore belong to *Brachypotherium* there remain a number of lower jaw fragments with teeth and isolated lower teeth that have the groove externally between meta- and hypolophid. Although they are very similar in size to those of *Dicerorhinus* they do not necessarily belong to that genus. They may in part represent *Aceratherium* (the lower molars of *Aceratherium* cannot be distinguished from those of *Dicerorhinus*), and some of them may even represent *Brachypotherium* if the flattened outer groove is not constant in the Rusinga and Karungu *Brachypotherium*. However, since *Dicerorhinus* is the most common of the East African Miocene rhinoceroses, most of the lower teeth probably belong to that genus, and are enumerated below:

No. 786, 1948, West Hiwegi, Rusinga, left mandibular ramus with P_3-M_3, teeth all fractured and incomplete, P_4 slightly worn, M_3 erupting,

No. 788, 1948, West Hiwegi, Rusinga, a right ramus, teeth broken off,

No. 1063, Kiahera Hill, Rusinga, P_2 sin.,

No. 990, 1950, Gumba Rusinga, P_3 dext.,

No. 1397, 1950, Rusinga, M_1 dext.,

No. 223, 1949, Wakondu, Rusinga, right ramus fragment with M_{2-3},

No. 429, Ngira, Karungu, unerupted crowns of P_{2-4} dext., slightly worn M_1 dext., and unworn incomplete crown of M_2 dext.,

No. 596, 1947, junction R.1 and R.1a, Rusinga, left ramus with M_{2-3},

Five isolated teeth, all marked RS, Rusinga, representing the left P_4 and the right and left M_{2-3}, all much worn down,

No. 342, 1950, Ngira, Karungu, incomplete P_3 dext.,

A ramus fragment marked " Aloir, '39, Owen " bears the damaged crowns of the left P_4 and M_1,

A ramus fragment marked " Karungu, 1937, Owen" has a much worn left M_2 that is incomplete externally behind,

Nos. 84–86, 1950, R.1–1a, Rusinga, incomplete P_4 and M_{2-3} dext., possibly belonging together,

F.3062 and F.3057 are two portions of a left lower molar from Rusinga,

No. 83, 1950, R.1–1a, Rusinga, a much worn and incomplete M_1 or M_2 sin.

M_1 is wider behind than in front. In M_2 the posterior lophid is either wider or narrower than the anterior, and in M_3 either the width is greatest in front, or (no. 231 ; Table 5) there is no difference between anterior and posterior width. M_3 is further characterized by the slight development of the posterior cingulum and (but this only upon a certain amount of wear) the absence of a posterior pressure scar. Measurements of the Rusinga and Karungu specimens are given in Table 6.

TABLE 6

Measurements of lower teeth from Rusinga and Karungu (mm.)

	no. 786	no. 1063	no. 429	RS	no. 342	nos. 84–86
P_2, ant. post.	—	27	28	—	—	—
ant. transv.	—	16	15	—	—	—
post. transv.	—	19	18	—	—	—
		no. 990				
P_3, ant. post.	—	35	—	—	—	—
ant. transv.	—	20	—		21	—
post. transv.	23	22	—	—	23	—
					Aloir '39	
P_4, ant. post.	39	—	38	—	—	38
ant. transv.	—	—	25	24	—	—
post. transv.	26	—	27	27	25	—
		no. 1397				
M_1, ant. post.	—	42	44	—	—	—
ant. transv.	26	26	27	—	—	—
post. transv.	—	28	31	—	—	—
		no. 223	no. 596		Karungu '37	
M_2, ant. post.	—	43	—	42	47	45
ant. transv.	29	28	26	29	31	—
post. transv.	27	29	27	29	—	28
M_3, ant. post.	—	45	44	46	—	—
ant. transv.	—	29	27	28	—	30
post. transv.	—	26	26	27	—	—

For the sake of completeness I mention the lower molar fragments that comprise only the hypolophid, and do not show whether the groove between it and the metalophid was deep or flattened. These are R.106, Rusinga; no. 346, 1950, Ngira, Karungu; no. 446, Kachuku, Karungu, and F.3051, Rusinga. The last two are posterior portions of M_3, right and left, and 26–28 mm. wide. Nothing can of course be said as to the generic position of these fragments.

In the British Museum (Natural History) there is a set of upper milk molars, DM^{1-4} sin., *in situ* in a maxillary, very well preserved, and marked Rs.26, Rusinga (Pl. 5, fig. 1). DM^1 is a small triangular tooth the ectoloph of which bears a vertical ridge in the middle, the mesostyle. The protocone, which is placed internally at the same level as the mesostyle, is an isolated cusp. The front part of the crown narrows anteriorly and is bounded lingually by a low ridge and buccally by the ectoloph crest, which unite at the antero-external angle so as to enclose a shallow fossa. The hypocone behind the protocone is connected with the metacone by a low ridge separating the medisinus from the postsinus. DM^2 has a mesostyle (not present in the more posteriorly placed milk molars or in the permanent dentition). The protoloph and the metaloph are damaged internally but appear to be equally long transversely. Both the paracone style and the metacone style are weak. The entrance to the medisinus is low and V-shaped. There is a crista united with the crochet, closing off a medifossette. DM^3 has no crista, and the crochet extends only half way across the medisinus. The ectoloph is depressed between the roots. The paracone style is only in part preserved and the parastyle has broken off. The medisinus entrance is wider than that in DM^2 and likewise unobstructed. The grooves delimiting the protocone are faintly shown. DM^4, of which the paracone style is incomplete, has the valley entrance again wider, the crochet longer, but the protocone constriction as little developed as in DM^3. The anterior cingulum is more prominent, but, like in DM^3, it does not quite extend to the antero-internal crown angle. There is no trace of a cingulum internally. The posterior moiety of the ectoloph with the faint metacone style is much more inclined inward than the anterior half.

The DM^4 of the Rusinga milk dentition agrees so well with the M^1 of the *Dicerorhinus* dentitions from Rusinga, differing mainly in lesser size (Table 7) and thinner enamel, as may be expected, that the juvenile Rusinga specimen may also be referred to *D. leakeyi*.

TABLE 7

Measurements of upper milk teeth of *Dicerorhinus leakeyi* (mm.)

DM^1, ant. post.	24	DM^3, ant. post.	32
transv.	20	ant. transv.	37
DM^2, ant. post.	26	post. transv.	35
ant. transv.	*c.* 30	DM^4, ant. post.	36
post. transv.	*c.* 30	ant. transv.	40
		post. transv.	39
		p. tr. : a. tr.	0·98

There are two specimens of DM^4 from Rusinga that should be referred to *Acera-therium*, and they will be dealt with later. There are also a much worn right DM^1 (no. 546, 1950, R.3, Rusinga) with a length of *c.* 25 mm. and another DM^1 dext. from Rusinga that is 22 mm. wide.

The upper milk dentition of *D. schleiermacheri* as figured by Kaup (1834, pl. 11, fig. 7) is larger than that of *D. leakeyi* ; the overall length of DM$^{2-4}$ is 120 mm. as opposed to 103 mm. in the Rusinga specimen, and the width of DM^3 is 40 mm., that of DM^4 42 mm. (Kaup (1834 : 37) gives 52 mm. for the width of DM^4, but a cast of the figured specimen in the British Museum (Natural History), no. 110b (O.C.), shows it to be 42 mm.). The crochet is better developed in the Eppelsheim milk teeth than in those from Rusinga. The milk dentition of *D. sansaniensis* (Pavlow 1892, pl. 5, fig. 8) has a length DM$^{2-4}$ of 104 mm., and widths of DM^3 and DM^4 of 35 and 37 mm. respectively, as measured from the figures, slightly less than in *D. leakeyi*. The milk dentition of *D. primaevus* as given by Arambourg (1959 : 59) is larger than that of *D. leakeyi* (length DM$^{2-4}$ 123·5-131·5 mm., width DM^3 42·5-45 mm., of DM^4 44–50·4 mm.). It is within these limits that falls the DM^4 of *Dicerorhinus* (?) spec. from the Pontian of Gravitelli, Sicily, the width of which is 47 mm. (Hooijer, 1946*c* : 322).

The lower milk dentition of *Dicerorhinus leakeyi* is best represented in a specimen from Napak V (August, 1962), Uganda, sent to me for identification by Dr. W. W. Bishop. It comprises DM$_{2-4}$ dext., with the crowns unworn; the metalophids of DM$_3$ and DM$_4$ are damaged apically behind. The posterior valley of DM$_2$ is closed inside, the anterior valley of DM$_3$ nearly so. In DM$_3$ the metalophid is bilobed in front, the parastylid well developed (Pl. 4, fig. 1). This dentition tallies well in size with the upper milk dentition of *Dicerorhinus* from Rusinga and may be referred to the same species. There are more remains of the lower milk dentition from Karungu and Rusinga some of which present larger dimensions than the Napak specimens, but the difference is small. These are:

No. 429, Ngira, Karungu, right DM$_3$ and part of DM$_4$ in a ramus fragment (this number also includes the unerupted premolars evidently of the same individual),

No. 405, 1951, Rusinga, right ramus with DM$_{3-4}$ and erupting M$_1$,

No. 1580, 1950, Rusinga, part of left DM$_3$ in ramus fragment,

F.3058, Rusinga, posterior portion of DM$_3$ and anterior portion of DM$_4$ sin.,

F.3059, Rusinga, anterior portion of DM$_4$ dext., and

No. 485, 1948, Kathwanga, Rusinga, posterior portion of DM$_4$ sin.

Measurements of the lower milk molars are given in Table 8.

TABLE 8

Measurements of lower milk teeth from Napak, Karungu, and Rusinga (mm.)

	Napak V	no. 429	no. 405	no. 1580	nos. 3058/9 and 485
DM$_2$, ant. post.	27	—	—	—	—
ant. transv.	13	—	—	—	—
post. transv.	16	—	—	—	—
DM$_3$, ant. post.	37	36	40	—	—
ant. transv.	17	19	19	18	—
post. transv.	20	21	21	—	—
DM$_4$, ant. post.	34	—	37	—	—
ant. transv.	19	22	23	—	19
post. transv.	20	—	—	—	20

DM$_2$ in *D. schleiermacheri* (Kaup 1834 : 38, pl. 11, fig. 10) measures 28 mm. anteroposteriorly and 15·5 mm. in width; it has the posterior valley closed inside. The various milk dentitions of *D. primaevus* (Arambourg 1959 : 63) are larger than the East African DM$_{2-4}$ except in the width of DM$_2$ which is given as 13·5–15 mm.; the width of DM$_3$ is 22–26 mm., and that of DM$_4$ 23·5–26·5 mm. The posterior valley of DM$_2$ is open inside, making it a narrow tooth in *D. primaevus*, but as observed by

Arambourg (1959 : 62) the valley may be either open or closed in DM_2 of *D. schleiermacheri*, and this varies in the Recent species also : the posterior valley in DM_2 becomes either shallower or deeper as it passes outwards. In the latter case it may become isolated as an enamel island upon wear and show a lingually closed valley (Hooijer 1946*a* : 32).

Genus ***ACERATHERIUM*** Kaup 1832

Aceratherium acutirostratum (Deraniyagala)

(Pl. 3 ; Pl. 4, figs. 2, 3 ; Pl. 5, figs. 4, 5 ; Pl. 6, figs. 1–4 ; Pl. 9, figs. 2–4 ; Pl. 14, figs. 4, 5)

1951*a* *Turkanatherium acutirostratus* Deraniyagala : 24.
1951 *Turkanatherium acutirostratus* Deraniyagala : 134, pl. 1.
1953 *Turkanatherium acutirostratus* Deraniyagala ; Deraniyagala : 13, pl. 1 ; pl. 2, figs. *b*, *c* ; pl. 3, figs. *b*, *d*.

The skull from Moruaret Hill near Losodok described by Deraniyagala (1951, 1953) as *Turkanatherium acutirostratus* has elongate, weak nasals and a weak double sagittal crest. There is neither a nasal nor a frontal horn. The premaxillaries are well developed and, although incomplete, extend forward beyond the nasals. They evidently carried incisors, but these are lacking. The occiput is elevated, giving a concave fronto-parietal profile. The dentition of the Turkana skull is characterized by the antecrochet blocking the medisinus in the premolars, which have a prominent internal cingulum, and a markedly constricted protocone and strong antecrochet in the molars. These are characters occurring in *Aceratherium*, and I have recently described a number of teeth from the Miocene of Congo as *Aceratherium acutirostratum* (Deraniyagala) (Hooijer 1963 : 43, pl. 6, figs. 1–3 ; pl. 7, figs. 1, 3–5, 8 ; pl. 8, fig. 2). Earlier, Arambourg (1959 : 74) had already stated that *Turkanatherium* appeared to be a synonym of *Aceratherium*.

There are various *Aceratherium* species in the Tertiary of Europe known by more or less complete skulls, and the Turkana *Aceratherium* may be compared with these. The high occiput is found only in the Pontian *Aceratherium incisivum* (Kaup 1834, pl. 10, fig. 2) ; in the earlier species the occiput is less elevated (see Wang 1928, text-fig. 1). *Aceratherium incisivum*, as first discovered by Osborn (1899), has a frontal horn, of which there is no evidence in *Aceratherium acutirostratum* or in the pre-Pontian European species. Elongate weak nasals are common in *Aceratherium* ; those in the Turkana skull appear to agree best with those of *Aceratherium lemanense* (Pomel) (Mermier 1896, pl. 1). In this Stampian and Aquitanian species the naso-maxillary notch extends backward only to above the middle of P^3, as in the Turkana skull ; in *Aceratherium platyodon* Mermier of the Burdigalian and in *Aceratherium tetradactylum* (Lartet) of the Vindobonian the notch extends backward to above the middle of P^4, whereas in *A. incisivum* it extends to above the front of M^1 (Mermier 1896, pl. 1 ; Breuning 1924 : 13). In the Turkana skull the anterior border of the orbit is above the anterior border of M^2, as in *A. lemanense, A. platyodon*, and *A. tetradactylum* ; in *A. incisivum* it is above the middle of M^2 (Mermier 1896, pl. 1).

Aceratherium lemanense has a true sagittal crest (skull from Gannat figured by Roman 1912, pl. 8, figs. 1, 1*a*) as well as one of the *Aceratherium incisivum* skulls (Kaup 1834 : pl. 10, fig. 2*a*) ; in the other skull of *A. incisivum* (Kaup 1834, pl. 10, fig. 2*b*) the fronto-parietal crests do not meet.

In the collection from R.1, Rusinga, there are remains of an *Aceratherium* skull, numbered 850, 1947. Unfortunately the skull is in fragments, and it has been possible only to assemble the nasals (Pl. 9, fig. 3) and the fronto-parietal portion of the skull, not fitting together. In restoring these from the fragments both parts appeared to be distorted by pressure mostly from the right side. The nasals evidently did not carry a horn : there is no eminence or rugosity but a groove in the median line instead. The length from the tip to the beginning of the downward curve for the naso-maxillary notch is 14 cm. ; the width of the nasals from 5 cm. behind the blunt tip backward to the narial notch is only 8 cm. throughout. Thus, the nasals are long and slender, as in *A. lemanense*. The fronto-parietal portion shows at least the absence of a true sagittal crest ; the least distance between the two fronto-parietal crests is $4\frac{1}{2}$ cm., as in one of the *A. incisivum* skulls referred to above. There are no indications of the presence of a frontal horn in the Rusinga skull. Neither the greatest width at the postorbital processes nor the dorsal profile can be made out from the Rusinga specimen.

Of the upper dentition of skull no. 850 only a few fragments remain, and they do not show any characteristic features except for one that shows a pit inside the cingulum at the medisinus entrance ; all the crown fragments are much worn down. The mandible of the skull is preserved, but much fragmented and distorted. The symphysial portion is poorly preserved, and the canine alveoli cannot well be traced. The rami are incomplete below, and nothing is preserved of the postdental portions except for the tip of the left coronoid process. The dentition, P_3–M_3 of both sides, is well worn down, and will be dealt with later.

The upper dentition of *Aceratherium* is less well represented at Rusinga than is that of *Dicerorhinus* ; there are, however, a few characteristic premolars. Two specimens, nos. 231 and 232, 1950, R.2–4, Rusinga, comprise a P^4 dext. with part of the M^1 attached to it, and a P^4 sin. of the same individual. The antero-external corners of both premolars are broken off (Pl. 6, figs. 1–4). The P^4 is worn down slightly less than in the *Dicerorhinus* dentitions, viz., to 16 mm. from the internal enamel base (the M^1 is worn down to 10 mm. ; it erupts earlier than the P^4). There are marked differences between the P^4 of nos. 231–232 and those of *Dicerorhinus*. The inner entrance to the medisinus is much lower in nos. 231–232, obstructed only by a ridge 8 mm. high, forming part of the inner cingulum, slightly rising behind and bordering a shallow pit. The bottom of the medisinus, which is only 7 mm. above the internal base of the enamel of the crown just inside the cingulum, rises inside the tooth (toward the external side) over a horizontal distance of 12 mm. to a level of 16 mm. above the enamel base. At this point the antecrochet extends completely across the medisinus. Buccally of the antecrochet the medisinus deepens again, and changes its course from transverse to obliquely forward and outward. The constriction of the protocone by anterior and posterior grooves is very marked.

The differences may be tabulated as follows :

Dicerorhinus P^4	*Aceratherium* P^4
proto- and metaloph united internally up to at least 15 mm. from crown base ; internal cingulum weakly developed ; protocone constriction slight.	medisinus open lingually to 7 mm. from crown base ; internal cingulum prominent, forming ledge between proto- and metaloph ; marked protocone constriction ; antecrochet prominent.

The type of P^4 represented in the sample nos. 231–232 is that of *Aceratherium acutirostratum* as described and figured from the Miocene of the Western Rift, Congo (Hooijer 1963 : 43, pl. 6, figs. 1–3 ; pl. 8, fig. 2). The Congo P^4 is less worn than the Rusinga specimens, and somewhat larger. It has a more developed internal cingulum, a ridge about 12 mm. high, at which level the medisinus opens internally, and extending along the protoloph, too. Some 14 mm. inside the tooth the medisinus is blocked completely by a narrow antecrochet. The constriction of the protocone is marked.

The following premolars should also be referred to *Aceratherium* :

No. 991, 1950, Gumba, Rusinga, P^2 sin., external portion missing ; heavy cingulum internally,

Two specimens in the British Museum (Natural History), one marked Rs.91, Rusinga, P^3 dext., slightly worn, inner cingulum only at medisinus entrance, narrow antecrochet across the medisinus, and the other a much worn P^3 sin. from R.1, Rusinga, with internal cingulum almost absent but antecrochet across medisinus,

F.3054 and F.3063 (one specimen), Rusinga, P^3 dext., worn and incomplete but showing the pit inside the inner cingulum at medisinus entrance,

No. 187, 1947, South of Kiahera Hill, Rusinga, P^3 dext., worn and corroded, showing protocone constriction and antecrochet across medisinus,

K.343, 1950, Ngira, Karungu, a P^3 or P^4 dext., sides broken off except internally, showing pit inside cingulum.

Measurements are given in Table 9.

TABLE 9

Measurements of upper premolars of *Aceratherium acutirostratum* (mm.)

	Lake Albert, Congo	nos. 231–232	Rs.91	R.1
P^3, ant. post.	—	—	—	32
ant. transv.	—	—	—	46
post. transv.	—	—	38	42
P^4, ant. post.	46	—	—	—
ant. transv.	60	—	—	—
post. transv.	53	46	—	—

The upper molars of *Aceratherium acutirostratum* from Lake Albert, Congo (Hooijer

1963 : 43, pl. 7, figs. 1, 3–5, 8) are larger than those of *Dicerorhinus leakeyi* and differ in the protocone being markedly constricted off. Immediately external to the posterior protocone fold the antecrochet bulges out and basally extends all across the medisinus as seen in the figured M^1. This is not the case in *Dicerorhinus*. The anterior cingulum is strongly developed and encroaches upon the internal surface of the protoloph. The M^3 differs from that of *Dicerorhinus* in that the metacone bulge is not developed, making the crown triangular rather than trapezoid, and in the protocone being markedly constricted. The Congo M^3 is unworn at the paracone, and the height of the crown at this point (49 mm.) is much less than the length of the outer surface (65 mm.), making this a brachyodont tooth (cf. Cooper 1934 : 575–581). No unworn M^3 of *Dicerorhinus leakeyi* is available, but from the amount of crownward convergence of the parastyle and metastyle the relative height of the external surface does seem to be much the same as that in *Aceratherium acutirostratum*.

Upper molars of *Aceratherium* from Rusinga comprise three specimens only:

No. 231, 1950, R.2–4, Rusinga, anterior portion of M^1 dext. adhering to P^4 (Pl. 6, figs. 3, 4),

No. 1630, 1950, Rusinga, upper M. dext., damaged on all sides but medisinus complete, and

No. 515, 1951, Rusinga, upper M sin., ectoloph and most of metaloph missing.

Among the rhino material from Napak, Karamoja, Uganda, sent to me by Dr. W. W. Bishop there is a specimen (no. 502, Napak I, 1958 (13)) showing the inner portion of the protoloph of a right upper molar with a deep protocone fold and an antecrochet all across the medisinus. This specimen represents the *Aceratherium* from Congo and Kenya.

Of the upper molars from Rusinga no measurements can be given, but some of the premolars are smaller than those from Congo. All are, however, characterized by the antecrochet extending all across the medisinus. The inner cingulum is stronger in some than in others. This varies among the European species of *Aceratherium* also.

In the British Museum (Natural History) there is a cast of a left upper dentition of *Aceratherium lemanense* from Auvergne (M.29624). I have compared this with upper dentitions of *Aceratherium incisivum* in the same museum, viz., a cast of the skull figured by Kaup (1834, pl. 10, fig. 2) with the teeth well preserved (M.2781), a left P^2–M^3 (Enniskillen collection, M.233), a left P^{2-4} (Hastings collection, M.27464), and an isolated M^3 dext. (Enniskillen collection, M.2370). All are from Eppelsheim. As shown in Table 10 the dentition of *A. lemanense* is similar in size to those of *A. incisivum*, but the postero-transverse diameter of M^1 and M^2 is equal to the antero-transverse diameter, and M^3 is relatively larger. Other primitive characters shown in the *A. lemanense* dentition are the stronger inner cingulum and the absence of crista and crochet. In both, however, we find the strong antecrochet and protocone constriction typical of *Aceratherium* molars. The crista is variously developed in *A. incisivum* : there are traces in P^3 and P^4 in M.2781 and M.233 ; it is more developed in M.27464, even forming a medifossette with the crochet in P^2. In the figured dentition (Kaup 1834 : pl. 14, fig. 5) there is a medifossette in P^4 as well. The crochet is well developed in the molars, and in M.2370 even forms a medifossette with the crista. The internal cingulum of the premolars either is confined to the medisinus entrance or extends forward and backward from this point.

TABLE 10

Measurements of upper teeth of *Aceratherium* (mm.)

	A. lemanense	*A. incisivum*		
	M.29624	M.2781	M.233	M.27464
P^2, ant. post.	31	31	32	26
ant. transv.	40	42	39	35
post. transv.	42	45	43	—
P^3, ant. post.	34	34	37	31
ant. transv.	52	54	53	47
post. transv.	50	53	51	44
P^4, ant. post.	39	35	38	37
ant. transv.	56	59	52	51
post. transv.	53	56	49	46
M^1, ant. post.	39	41	42	
ant. transv.	55	60	54	
post. transv.	55	57	49	
p. tr. : a. tr.	1·00	0·95	0·91	
M^2, ant. post.	43	44	45	
ant. transv.	58	63	58	
post. transv.	58	60	—	
p. tr. : a. tr.	1·00	0·94	—	M.2370
M^3, ant. post.	47	44	44	44
ant. transv.	58	59	51	55
l. outer surface	65	61	57	56

The *Aceratherium* dentition from Congo certainly resembles that of *A. incisivum* more than that of *A. lemanense*; there is a well-developed crochet, and at least a trace of a crista in P^4, the M^1 and M^2 are narrower behind than in front (ratios 0·90 and 0·89, respectively), and M^3 is less wide than M^2 (Hooijer 1963 : 43). However, not all of the *A. lemanense* dentitions are as primitive-looking as that mentioned above, and even the antecrochet is not constant. The latter is well developed across the medisinus in the premolars of the dentition from Cindré (Allier) figured by Roman (1912 : 59, pl. 8, fig. 2*a*), but may be much reduced or absent as in the dentitions figured by Osborn (1900 : 242, text-fig. 8B) and by Viret (1929 : 258, pl. 27, fig. 2). Again, the prominent antecrochet blocking the medisinus in the premolars is seen in "*Teleoceras aquitanicum*" Repelin (1917 : 37, pl. 5, figs. 7, 8), which is probably the same as *A. lemanense* (Wang 1928 : 207), as well as in the Burdigalian *Aceratherium platyodon* (Mermier 1896, pl. 2, fig. 4), but it is absent in the premolars of "*Teleoceras aginense*" Repelin (1917 : 12, pls. 1, 3, 4), which, as pointed out by Lavocat (1951 : 114) is identical with *Aceratherium lemanense*. Also, the first and second molars of *A. lemanense* are not always as wide behind as in front as seen from the figures cited. In *A. tetradactylum* we find much variation in tooth size, development of antecrochet in the premolars, and the inner cingulum (Wang 1928 : 189). The teeth of this

Vindobonian species are close to those of the Pontian *A. incisivum* with which it has often been united.

The lower canines numbered 850, 1947 (R.1) (Pl. 4, figs. 2, 3) belong to the same individual and differ from those of *Dicerorhinus* in being curved, with the convex sides facing each other. The diameters at crown base are 32 mm. horizontally and 24 mm. vertically. The cross-section is a transverse oval, and the diameters of the root are 28 by 23 mm. This pair agrees with *Aceratherium* in curvature and cross-section; the root length is over 11 cm., more than in a specimen of *A. tetradactylum* from Georgensgmünd recorded by Wang (1928 : 189, text-fig. 2A) that has nearly the same diameters. In *A. incisivum* (Kaup 1834 : 52, pl. 14, fig. 9) the lower canines are much larger (length 27–30 cm., width 38–44 mm.), and very large lower C are also known in the Aquitanian *A. lemanense* (Repelin 1917 : 24, pl. 5, fig. 3). The flattening of the canine in *A. acutirostratum* is less marked than in *A. platyodon* (Mermier 1895, text-fig. 5) but more than in *A. incisivum* (Mermier 1895, text-figs. 6–8).

The only premolars and molars of the lower jaw that may be referred to *Aceratherium acutirostratum* are those in the poorly-preserved mandible numbered 850, 1947, belonging to the skull remains mentioned above (Pl. 9, fig. 4). The teeth are much worn down, devoid of external cingula and with a sharp groove between meta- and hypolophid. They cannot be distinguished from those of *Dicerorhinus leakeyi* (Table 5) but P_3, M_2 and M_3 are slightly longer. In Table 11 the Rusinga teeth may be compared for size with those of *A. tetradactylum* (no. 1 after Filhol 1891 : 204 (Sansan), nos. 2–4 after Wang 1928 : 190 (Georgensgmünd), and no. 5 after Rinnert 1956 : 33 (Viehhausen)). The lower teeth of *A. incisivum* recorded by Kaup (1834 : 53, pl. 14, fig. 9) are not very large either.

TABLE 11

Measurements of lower teeth of *Aceratherium* (mm.)

	A. acutirostratum no. 850	*Aceratherium tetradactylum*					*A. incisivum*
		1	2	3	4	5	
P_3, ant. post.	36	31	33	30·5	30	32	30
ant. transv.	20	23	20	14	16	18	—
post. transv.	22	—	15	21	21	20·5	26
P_4, ant. post.	—	36	36	33	35	34	33·5
ant. transv.	25	27	23	25	22	22	—
post. transv.	26	—	18	26	23	24	26
M_1, ant. post.	—	37	37	34	35	37·5	34
ant. transv.	26	27	20	23	22	24·8	—
post. transv.	29	—	—	27	26	25·6	25
M_2, ant. post.	48	40	38?	42	37	40·5	34
ant. transv.	30	29	22	25	25	27	26
post. transv.	31	—	—	27	25	27·2	—
M_3, ant. post.	53	42	38	43	47	42	39
ant. transv.	30	27	19	25	22	28	25
post. transv.	29	—	20	26·5	24	28	—
Length P_2–M_3	*c.* 240	215	—	216	220	—	205

Of the milk dentition of *Aceratherium acutirostratum* there are two specimens, both DM^4: no. 142, 1949, Kamasengere, Rusinga, DM^4 dext. (Pl. 5, fig. 4), and no. 218, 1948, R.107, Rusinga, DM^4 sin (Pl. 5, fig. 5). They differ from their homologue in the *Dicerorhinus* dentition from Rs.26 in having the protocone well defined. The anterior cingulum extends to the internal angle of the crown, the antecrochet is conspicuously developed, and the crochet is smaller. The parastyle is broken off in no. 218. These milk molars agree so closely with M^1 of *Aceratherium acutirostratum* in their antecrochet and cingular development and in the degree of individualization of the protocone that they may safely be regarded as *Aceratherium*. They are also larger than the *Dicerorhinus* DM^4 as will be seen by comparing Table 12 with Table 7.

TABLE 12

Measurements of upper milk molars of *Aceratherium acutirostratum* (mm.)

	no. 142	no. 218
DM^4, ant. post.	40	38
ant. transv.	47	48
post. transv.	45	44
p. tr. : a. tr.	0·95	0·92

Genus ***BRACHYPOTHERIUM*** Borissiak 1927

Brachypotherium heinzelini Hooijer

(Pl. 4, fig. 6; Pl. 6, figs. 5, 6, 9; Pl. 7, figs. 3, 4; Pl. 8; Pl. 9, fig. 1; Pl. 10, figs. 1–3, 6–8; Pl. 14, fig. 3)

1963 *Brachypotherium heinzelini* Hooijer: 45, pl. 6, figs. 4–6; pl. 8, fig. 1.

A right upper incisor, no. 79, 1950, R.1–1a (Pl. 4, fig. 6) lacks only a portion of the root. The crown diameters are 78 mm. anteroposteriorly and 24 mm. transversely. The root is hardly higher than the crown length. This specimen, much larger than the upper I referred to *Dicerorhinus leakeyi* (Table 2), agrees well with an upper incisor of *Brachypotherium goldfussi*[1] (Kaup 1854: 2, pl. 1, fig. 13: 81 by 26 mm.), which also has a short massive root. Large incisors referred to *Aceratherium incisivum* (Kaup 1834: 51, pl. 14, figs. 1–4; 1854: 9, pl. 1, figs. 6–9) have the root higher than the crown length. If this differential character may be relied upon, the Rusinga incisor should be referred to *Brachypotherium*. Such large upper incisors have also been found at the type site of *Brachypotherium heinzelini* (Sinda no. 15) and another site, Lake Albert no. 446, from which a characteristic tooth of this species has been derived (Hooijer 1963: 47, pl. 7, fig. 2).

There are two sets of P$^{3-4}$ from Rusinga that should be referred to the present species, viz., no. 270, 1949, R.73, Rusinga, P^{3-4} dext. (Pl. 8, figs. 5, 6), and no. 409, 1947, West side of Hiwegi, Rusinga, P^{3-4} sin. (Pl. 8, figs. 3, 4).

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[1] This Pontian Eppelsheim *Brachypotherium* is considered merely a large variety of *B. brachypus* (Lartet) of the Vindobonian by Depéret (1887: 226). The upper incisor figured with the dentition of *B. brachypus* by Depéret (1887, pl. 23, fig. 3) has a slender and long root. It has been considered probably referable to *Aceratherium* by Rinnert (1956: 38), and is placed with "*Dicerorhinus*" (= *Aceratherium*) *simorrensis* (Lartet) by Viret (1961: 67).

The Rusinga premolars of *Brachypotherium* agree with the type of *B. heinzelini* Hooijer (1963 : 45, pl. 6, figs. 4–6 ; pl. 8, fig. 1) in the flattening of the ectoloph behind the paracone style (the metastyle of P^4 in no. 270 is missing), in the development of the inner cingulum (weaker in no. 409 than in no. 270 in which latter it forms a ridge and not a mere tubercle), and in the slight development of the antecrochet, which does not block the medisinus. The external cingulum, however, so markedly developed in the holotype, is only weak in no. 409, and virtually absent in no. 270. Variations in the development of the external cingulum have been noted in *B. brachypus* also (Viret 1961 : 69).

An isolated P^4 sin. originating from Napak IIC, Karamoja, Uganda, collected and sent to me by Dr. W. W. Bishop in 1964, unmistakably belongs to *Brachypotherium heinzelini*. The specimen (Pl. 8, fig. 1) has the crown surface broken and distorted externally and behind the medisinus, but the protoloph is well preserved, showing the weakly developed antecrochet and the tubercle at the medisinus entrace in which it agrees perfectly with the type P^4. The damage to the ectoloph notwithstanding it is clear that there was no external cingulum (well developed in the holotype, weak or absent in the Rusinga P^4). The basal diameters that can be exactly taken (Table 13) are intermediate between those of the two Rusinga P^4.

Neither in P^3 nor in P^4 of *B. heinzelini* the antecrochet is as strongly developed as in *B. aurelianense* (Nouel) of the Burdigalian (see Osborn 1900 : 250, text-fig. 11 ; Mayet 1908 : 100, text-fig. 29, pl. 1, figs. 1, 3[1]). In *B. brachypus* of the later Vindobonian the antecrochet in P^{3-4} is reduced or wanting (Osborn 1900 : 25), although the upper dentition of *B. brachypus* from La Grive Saint-Alban figured by Depéret (1887, pl. 23) is only slightly worn and therefore does not show much of the antecrochet, which becomes more marked toward the base as seen in the right upper molar figured (Depéret 1887, pl. 23, fig. 2). The external cingulum, absent in *B. aurelianense*, is either present or reduced in *B. brachypus* (Viret 1961 : 69). The criterion of the internal cingulum, present in *B. brachypus* and weak or absent in *B. aurelianense*, is not absolute (Viret 1961). As we shall see further on, the external cingulum is either present or absent in the upper molars of *B. heinzelini*.

The first and second upper molars of *Brachypotherium* are rare in the East African Miocene. There is a much worn M^1 dext. from Karungu, 1937 (Pl. 6, figs. 5, 6) that has the characteristic, if not constant, feature of the species, the external cingulum. The M^2 sin. from the Sinda area, Lower Semliki, Congo, described and figured by me as *Aceratherium* cf. *tetradactylum* (Lartet) (Hooijer 1963 : 44, pl. 8, figs. 4–6) belongs here, too. It does lack the external cingulum, and has been identified thus because of its marked resemblance to certain large molars from Beaugency and Pontlevoy figured by Mayet (1908 : 96, 271, pl. 3, fig. 7 ; pl. 10, fig. 4) as *Aceratherium* aff. *tetradactylum*, and *Aceratherium tetradactylum* mut. *pontileviensis*, respectively. However at the time I overlooked the fact that Stehlin (1925 : 108) had referred these to

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[1] And also Mayet 1908 : 100, text-fig. 30 : *Diceratherium douvillei* Osborn that would be based on female specimens of *Brachypotherium aurelianense* (Stehlin 1925 : 113).

Brachypotherium brachypus. Stehlin notes that in their morphological characters these supposed *Aceratherium* molars do not differ from those of *Brachypotherium brachypus*, and further that their large size is no valid reason for referring them to *Aceratherium tetradactylum*, which is smaller than *Brachypotherium brachypus.* Moreover, Stehlin notes that in the Pont-Levoy-Thenay deposits there is only one type of lower molar of corresponding size, belonging to *Brachypotherium.* Therefore, the M^2 from Sinda no. 2 should have been referred to *B. heinzelini.* The Congo molar differs from those of *Brachypotherium brachypus* compared in the internal cingulum being weaker (manifested by a large tubercle at the medisinus entrance only), and the crochet being more developed.

There is one specimen of the last upper molar in the Kenya collection that is referable to *Brachypotherium heinzelini.* This is the M^3 dext. from Karungu described and figured but not specifically identified by Andrews (1914: 176–177, pl. 28, fig. 3). The specimen (M.10632 ; Pl. 7, fig. 3) is somewhat larger than that of *Aceratherium acutirostratum* from Lake Albert, Congo (Hooijer 1963 : 43, pl. 7, figs. 1, 3) in anterior width and the length of the outer surface (Table 13) but has the protocone only weakly constricted off, not by sharp grooves as in *Aceratherium.* It lacks the marked metacone bulge of *Dicerorhinus* from Rusinga in which M^3 is smaller still. The cingulum forms a mere ridge at the medisinus entrance but is otherwise absent internally. The antecrochet is weak, and so is the crochet, while there is a trace of a crista. The upward convergence of parastyle and metastyle as seen from the

TABLE 13

Measurements of upper teeth of *Brachypotherium* (mm.)

		B. heinzelini			
	B. brachypus	Sinda	Rusinga		Napak
	M.33527		no. 270	no. 409	
P^3, ant. post.	33	—	36	—	—
ant. transv.	51	—	54	—	—
post. transv.	52	—	54	56	—
P^4, ant. post.	37	49	—	48	—
ant. transv.	57	62	61	66	64
post. transv.	55	58	56	62	59
			Karungu		
M^1, ant. post.	51	—	—		
ant. transv.	70	—	62		
post. transv.	60	—	52		
p. tr. : a. tr.	0·86	—	0·84		
M^2, ant. post.	51	63	—		
ant. transv.	68	77	—		
post. transv.	59	63	—		
p. tr. : a. tr.	0·87	0·82	—		
M^3, ant. post.	56	—	55		
ant. transv.	68	—	65		
l. outer surface	73	—	68		

external side (Pl. 7, fig. 4) shows the brachyodonty or mesodonty of the crown. The M^3 of *Brachypotherium brachypus* (see Mayet 1909 : 25, text-figs. 11, 12, both from the right side) are indistinguishable from the Karungu specimen but are smaller (antero-transverse diameters 53–59 mm.). The M^3 dext. from Beaugency referred by Mayet (1908 : 98, pl. 3, fig. 6) to *Aceratherium* cf. *tetradactylum*, but which Stehlin (1925 : 108, footnote 1) states should be referred to *B. brachypus*, is larger (antero-transverse diameter 68 mm.).

The left upper tooth series of *B. brachypus*, the measurements of which are given in Table 13, is from Villefranche d'Astarac (Gers), M.33527, and is made up of teeth of different individuals (the molar placed as M^2 is more worn than that in the place of M^1) but shows the characteristic features of the species. There are external as well as internal cingula in all premolars and molars ; the antecrochet is weak and the protocone constriction slight. The crochet is likewise weakly developed, and the crista is absent except for a trace in P^4. In the European species, however, the external cingulum may be reduced (Viret 1961 : 69), and so it is in some of the specimens of *B. heinzelini*. In size the African teeth agree rather well with those of *B. brachypus* : the premolars are larger than those of *B. brachypus* presented in the Table, but Viret (1961 : 69) cites a P^3 from La Grive 61 mm. wide, and P^4 68–70 mm. wide, exceeding the large Rusinga specimen no. 409, whereas the Sinda M^2 is larger, the Karungu M^1 and M^3 are however smaller than those in *B. brachypus*. The Sinda M^2 is relatively narrower behind than that in the *B. brachypus* dentition, but the M^1 of that dentition hardly differs from the Karungu M^1 in this respect.

The upper teeth of *Brachypotherium* are larger than those of *Dicerorhinus leakeyi* and *Aceratherium acutirostratum*, and differ further in being relatively narrower behind. Even when the external cingulum is absent the superior size and relatively smaller posterior width are distinctive of *Brachypotherium heinzelini*. The absence of a marked protocone constriction and of a large antecrochet differentiates *Brachypotherium heinzelini* molars from those of *Aceratherium acutirostratum*, while the flattened ectolophs, and the absence of the metacone bulge in M^3 serve to distinguish *Brachypotherium heinzelini* molars from those of *Dicerorhinus leakeyi*.

Although both Osborn (1900 : 250) and Mayet (1908 : 107) state that the external surface of the lower molars of the Burdigalian *B. aurelianense* is flattened, in actual fact this characteristic applies only to the more advanced brachypotheres. Most of the lower molars of *B. aurelianense* have a marked groove on the external surface between metalophid and hypolophid (Stehlin 1925 : 110, 111). In the Upper Burdigalian and Lower Vindobonian *B. stehlini* Viret (1961 : 71), which is generally larger than *B. aurelianense*, the lower molars have the external groove between meta- and hypolophid almost completely flattened out, and moreover almost invariably present an external cingulum (cf. Roman & Viret 1934 : 33, pl. 10, figs. 7, 8). The same characters are found in typical *B. brachypus* of the Upper Vindobonian (Viret 1961 : 72) in which the tendency toward hypsodonty is more marked, as well as in the terminal *B. goldfussi* (Kaup 1834 : 63, pl. 12, figs. 13, 14).

Few lower molars are present in the Rusinga, Karungu, and Napak collections in which the external groove is very shallow or nearly flattened out, and in none of them is there an external cingulum. These specimens doubtless belong to *Brachypotherium heinzelini*, but whether they are the only ones is not known ; some of the grooved specimens may also belong here if this character is not constant in the African species, as happens in *B. aurelianense*. One of the specimens definitely belonging to *Brachypotherium heinzelini*, that from Napak II A, 1964, is rather large, exceeding the *Dicerorhinus leakeyi* lowers in size ; the others are not particularly large. The specimens are as follows :

No. 546, 1949, R.1, Rusinga, posterior portion of M_1 or M_2 sin. (Pl. 6, fig. 9),
No. 345, 1950, Ngira, Karungu, posterior portion of M_1 or M_2 dext.,
Napak II A, 1964 (kindly forwarded by Dr. W. W. Bishop), M_2 sin., nearly entire (pl. 8, fig. 2), and
M.25186, R.7, Rusinga, M_3 sin., incomplete in front.

TABLE 14

Measurements of lower molars of *Brachypotherium heinzelini* (mm.)

	Rusinga no. 546	Karungu no. 345
M_1 or M_2, ant. post.	—	—
ant. transv.	—	—
post. transv.	29	31
	Napak II A	
M_2, ant. post.	56	
ant. transv.	37	
post. transv.	35	
	Rusinga M.25186	
M_3, ant. post.	—	
ant. transv.	31	
post. transv.	29	

No upper milk molars of *Brachypotherium* appear to be present in the East African Miocene collections. The DM^4 of *Brachypotherium* cf. *brachypus* from Chevilly figured as an M^2 of *Diceratherium douveillei* by Mayet (1908, pl. 3, fig. 5 ; see Stehlin 1925 : 114, footnote) has a stronger cingulum and the protocone less well marked off than the *Aceratherium* DM^4 of Rusinga.

The post-cranial skeleton of *Brachypotherium* is easily distinguished from that of *Dicerorhinus* and *Aceratherium* by the shortness and great relative width of the individual bones. All of the metacarpals are represented in the Rusigna collection:

M.18813 and M.18812, Rs.6a, Rusinga, associated Mc.III and Mc.IV dext. (Pl. 10, figs. 1, 2). Part of the shaft of the third metacarpal below the magnum facet medially is missing,
F.3269, R.VII.1941, Rusinga, Mc.II dext. (Pl. 10, fig. 3), and
M.18822, Rs.7, no. 451, 1947, Kathwanga, Rusinga, Mc.IV sin. (Pl. 10, fig. 8).

The median metacarpal is as much shortened as that in the Vindobonian *Brachypotherium brachypus*, whereas the second and fourth metacarpals from Rusinga are even relatively wider, and more shortened than their homologues in *B. brachypus*, as will be seen by comparing Table 15 with Table 16 (after Roger 1900 : 22).

TABLE 15

Measurements of metacarpals of *Brachypotherium heinzelini* (mm.)

	Mc. II F. 3269	Mc. III M. 18813	Mc. IV M. 18812	Mc. IV M. 18822
Median length	125	137	110	113
Proximal width	52	65	45	42
Proximal ant. post. diameter	47	51	53	46
Middle width	45	53	37	38
Middle ant. post. diameter	25	25	24	23
Greatest distal width	50	73	52	52
Width of distal trochlea	40	59	44	47
Distal ant. post. diameter	38	47	39	43

TABLE 16

Measurements of metacarpals of *Brachypotherium brachypus* (mm.)

	Mc. II	Mc. III	Mc. IV
Median length	100–132	130–147	116–130
Middle width	38–40	50–55	37–39

In *Brachypotherium stehlini* of the Upper Burdigalian of La Romieu the metapodials are longer than those in *B. brachypus* : Mc. II has a median length of 160 mm. by a middle width of 40 mm., and Mc. III has a median length of 170 mm., a proximal width of 70 mm. and the least width of shaft 53 mm. (Roman & Viret 1934 : 33, text-fig. 14, as *B.* cf. *brachypus* ; cf. Viret 1961 : 71). Thus, as already observed by Stehlin (1925 : 138), the *Brachypotherium* of the Burdigalian has the metapodials less shortened than that of the Vindobonian of La Grive, etc.

Of the *Brachypotherium* from the Miocene of Moghara in Egypt, described as *Teleoceras snowi* Fourtau, no metacarpal, but a left metatarsal III is available. This bone (Fourtau 1920 : 46, text-fig. 30) is longer than that in *B. brachypus*, and in fact is as long as that in *Brachypotherium stehlini* (Roman & Viret 1934 : 33, text-fig. 13A). The ranges of size in *B. brachypus* given in Table 17 are after Roger (1900 : 26) and Viret (1961 : 70).

TABLE 17

Measurements of metatarsal III of *Brachypotherium* (mm.)

	B. snowi	*B. stehlini*	*B. brachypus*	
Median length	151	150	110–137	105–112
Middle width	*c.* 50	55	45–50	47–51
Greatest distal width	67	72	up to 70	67

It follows from this that the Rusinga *B. heinzelini* is more progressive than that of Moghara in Egypt in having more shortened metapodials.

Among the isolated postcranial material from Rusinga there is one entire right radius, M.18908, Rs.6a, shorter and wider than the other radii recorded elsewhere in the present paper (Pl. 9, fig. 1). This bone very nearly agrees in dimensions with one of the Steinheim radii recorded by Roger (1900 : 17, table, no. 5) as *Brachypotherium.* The radius of *Brachypotherium stehlini* from La Romieu (Roman & Viret 1934 : 35, pl. 11, fig. 1) has the same proximal and distal widths but is much longer, as seen in Table 18.

TABLE 18

Measurements of radius in *Brachypotherium* (mm.)

	B. heinzelini Rusinga	*B. brachypus* Steinheim	*B. stehlini* La Romieu
Median length	293	300	357
Proximal width	95	98	99
Middle width	52	—	—
Greatest distal width	95	100	101

There are some twenty astragali in the East African Miocene collections, and of these there is one, from the left side, no. 538, Gumba, Rusinga, 1949 (Pl. 14, fig. 3) in which the total width greatly exceeds the medial height, nearly to the same extent as in the astragalus from the type site of *Brachypotherium heinzelini* (Hooijer 1963 : 47, pl. 5, fig. 10 ; pl. 8, fig. 7), and in *B. brachypus* (Table 19). In this Table, the La Grive specimen is after Depéret (1887 : 225, pl. 24, fig. 4), the Steinheim specimen after Roger (1900 : 24), M.33529 is from Villefranche d'Astarac, and M.7760 is a cast from Thenay (Loir-et-Cher). The Steinheim astragalus figured by Fraas (1870, pl. 7, fig. 6) is clearly *Brachypotherium* as already surmised by Depéret (1887 : 225), and so is the calcaneum of fig. 9 of Fraas's plate ; both are identified as *Rh. incisivus* by Fraas (1870 : 302).

TABLE 19

Measurements of astragalus of *Brachypotherium* (mm.)

	B. heinzelini		*B. brachypus*			
	Sinda	Rusinga	La Grive	Steinheim	M.33529	M.7760
Lateral height	—	57	—	73	—	—
Medial height	68	60	60	68	64	64
Total width	102	82	93	96	100	98
Ratio medial height/total width	0·67	0·73	0·64	0·71	0·64	0·65
Trochlea width	—	68	85	—	86	80
Width distal facets	—	71	85	—	85	85

The first phalanx of a median digit, F.2126, Rusinga, 1941 (Pl. 10, fig. 6), is shorter than any of its homologues in the East African Miocene collections, and moreover has a proximal width that represents the maximum in our series. The distal articular surface is evenly concave transversely, and flat anteroposteriorly instead of weakly convex as in the longer first phalanges. Its measurements are presented in Table 20 ; the data on *Brachypotherium brachypus* and on *Aceratherium* are after Roger (1900 : 27).

TABLE 20

Measurements of phalanx I, median digit (mm.)

	B. heinzelini	*B. brachypus*	*Aceratherium*
Length	28	28–30	35–45
Proximal width	55	53–55	45–57

The second phalanx of a median digit of *Brachypotherium heinzelini* is represented by no less than three specimens : F.2125, Rusinga, 1941 ; M.18854, Rs.101, Rusinga, and M.18862, Rs.6a, Rusinga (Pl. 10, fig. 7). These bones are shorter and wider than their homologues from Rusinga, and their proximal articular surface is evenly convex transversely and flat anteroposteriorly, not raised in the middle in front and behind as in the longer second phalanges. Measurements of *B. brachypus* and *Aceratherium* in Table 21 again after Roger (1900 : 27).

TABLE 21

Measurements of phalanx II, median digit (mm.)

	B. heinzelini				
	F.2125	M.18854	M.18862	*B. brachypus*	*Aceratherium*
Length	22	20	20	20	20–35
Proximal width	58	61	59	60	40–65

The phalanges from Viehhausen provisionally referred to *Brachypotherium* cf. *brachypus* by Rinnert (1956 : 37) appear to me to belong to either *Aceratherium* or *Dicerorhinus*.

The first phalanx of a lateral digit, M.18859, Rusinga, is relatively shorter and wider than the others, and agrees with F.2126 in the shape of the distal articular surface. It may therefore be referred to *Brachypotherium heinzelini*. The data on *B. brachypus* and *Aceratherium* given by Roger (1900 : 27) are few and apparently questionable ; I have added in Table 22 the measurements of some of the first phalanges of lateral digits from Rusinga, including those of the skeleton no. 2 from R.1, Rusinga, 1947.

TABLE 22

Measurements of phalanx I, lateral digit (mm.)

	B. heinzelini	*B. brachypus*	*Aceratherium*	Rusinga			
Length	28	(20–25)?	25–35	37	33	29	28
Proximal width	43	(50)?	45	40	38	35	40

There remains one second phalanx of a lateral digit, no. 1055, S. E. of Kiahera Hill, Rusinga, that is relatively wider than the others, and its proximal surface is evenly convex transversely as in *Brachypotherium*. The data on *B. brachypus* and *Aceratherium* in Table 23 are as given by Roger (1900 : 27); the data on some of the Rusinga second phalanges of lateral digits are added, including those of no. 2, R. 1, 1947.

TABLE 23

Measurements of phalanx II, lateral digit (mm.)

	B. heinzelini	*B. brachypus*	*Aceratherium*	Rusinga				
Length	22	(10–15)?	20–30	25	27	25	22	21
Proximal width	42	(47–50)?	45	39	37	35	37	27

This completes the account of the postcranial material from Rusinga referable to *Brachypotherium heinzelini*. The present species, first described from the Miocene of the Sinda-Mohari region, Lower Semliki, Congo (Hooijer 1963 : 45) on a P^4, the external cingulum of which has now been shown to be a variable feature, is more advanced than the European *Brachypotherium brachypus* which it resembles dentally, in the lateral metacarpals being more shortened and relatively wider.

Genus ***CHILOTHERIUM*** Ringström 1924

Chilotherium sp.

(Pl. 6, figs. 10, 11 ; Pl. 7, figs. 1, 2)

An M^3 dext. originating from Loperot 1948 (Pl. 7, figs. 1, 2) represents a genus not before recorded from the African Tertiary. It is well preserved, lacking only a small portion of the internal cingulum at the metaloph, and it is remarkable for two main features, viz., the great height of the crown, and the very weak development of the parastyle fold and the paracone style, characters not seen in *Dicerorhinus*, *Aceratherium*, or *Brachypotherium*.

The external surface of the M^3 (the joined ectoloph and metaloph) is peculiarly flattened and has the sides (parastyle and metastyle) much less converging crownward than in the other genera mentioned : the metastyle is slightly concave basally but becomes very nearly vertical at a level only 15 mm. from the base of the crown, while the parastyle is very steep also. The full basal length of the external surface is 61 mm., which length is reduced to 53 mm. at a height of 15 mm. from the enamel base, and still amounts to 46 mm. at 45 mm. from the base, at which level the crown is worn. Over this vertical distance the thickness of the ectometaloph has hardly reduced, and it is clear that the crown has already undergone a considerable amount of wear. The full height of the unworn crown may well have been some 25 to 35 mm. more than that to which it is worn down, that is, about 70–80 mm. The parastyle fold is hardly visible, and the paracone style is weakly developed in the upper portion of the crown, flattening out in the basal two-thirds. Near the base, there is a metacone bulge that is, however, placed nearer to the inner end of the external surface than in a *Dicerorhinus* molar. The protocone of the Loperot M^3 is very markedly defined and flattened internally; the anterior and posterior grooves delimiting it become sharper and deeper toward the base, where the posterior groove curves inward to end at the medisinus entrance. The antecrochet becomes very prominent basally, reducing the entrance to the medisinus to a narrow V, while the crochet, which nearly extends all across the medisinus apically, recedes towards the base. There is a weak crista, a projection from the ectoloph opposite the paracone, not yet touched by wear, not reaching the crochet, and like it receding basally. The cingulum is well developed along the anterior surface, absent along the inner surface of the protoloph, forming a cusp entering the medisinus, and continuing along the metaloph, rising to a point 15 mm. high at the metacone bulge posteriorly, beyond which it falls off steeply. There is no cingulum along the external surface.

The great hypsodonty of the Loperot M^3 and the flattening of the external surface as well as the very marked protocone constriction, prominent antecrochet, and metacone bulge near the internal angle, are all characters pointing to its belonging to the genus *Chilotherium* Ringström (1924 : 26). This remarkable genus of extinct rhinoceroses with its orbit near the upper surface of the skull, the exaggerated symphysis width and huge, widely separated canines had often been regarded as *Aceratherium* until Ringström (1924) recognized its true character and gave it separate generic status. The specimen from Loperot described above is exceedingly similar in shape and size to the M^3 of *Chilotherium anderssoni* Ringström (1924 : 34, 35, pl. 3, figs. 3, 4) from the Pontian of Shansi, North China. The length of the external surface of the M^3 of *C. anderssoni* is 58–60 mm., the anterior width 53–59 mm., and the full height of the crown, presumably the same as in M^2, about 85 mm. In *C. anderssoni* the metacone bulge is as in the Loperot M^3; in *C. habereri* (Schlosser) there is no bend at the junction of ecto- and metaloph, the external surface being evenly rounded throughout, and the posterior cingulum is more developed, free at its apex (Ringström 1924 : 41, pl. 4, fig. 3). *C. habereri* as well as the other species of *Chilotherium* described from Shansi and Shensi by Ringström are smaller than *C. anderssoni*. In the M^3 of *C. wimani* Ringström (1924, pl. 7, fig. 3) there is a slender crista uniting with the crochet; the internal cingulum is rather variable in the molars but invariably developed at the medisinus entrance.

Table 24 gives the measurements of the Loperot M^3 in conjunction with those of *Dicerorhinus leakeyi*, *Aceratherium acutirostratum*, and *Brachypotherium heinzelini*. While in size the *Chilotherium* M^3 exceeds its homologue in *Dicerorhinus*, it is near to the M^3 of *Aceratherium* and *Brachypotherium* in length, but less wide anteriorly and with the external surface shorter.

In the Rusinga collection there are two incomplete right upper molars that appear to belong to *Chilotherium* as well, viz.,

No. 695, 1949, Gumba, Rusinga, lacking outer portion (Pl. 6, fig. 10), and
No. 506, 1950, Wakondu, Rusinga, protoloph only (Pl. 6, fig. 11).

Both of these show the very markedly constricted and internally flattened proto-

TABLE 24

Measurements of M³ in various genera (mm.)

	Chilotherium sp. Loperot	*Dicerorhinus leakeyi* Rusinga	*Aceratherium acutirostratum* Lake Albert	*Brachypotherium heinzelini* Karungu
ant. post.	56	42–46	57	55
ant. transv.	60	50–54	62	65
l. outer surface	61	52–57	65	68

cone, delimited by grooves the posterior of which curves inward basally, the prominent antecrochet, the strongly developed anterior cingulum, and the cingular cusp entering the medisinus : the characters of the Loperot specimen. In the more complete specimen (no. 695) the medisinus is not very well preserved, the molar having been assembled from fragments, but from what is left of the crochet it is evident that it is very prominent, extending forward and outward beyond the antecrochet, as in *Chilotherium.* Moreover, the protoloph (no. 506) is less worn than that in the Loperot M³, the internal height of the protocone is 34 mm. Seen from the internal side its crownward taper is less marked than in either *Aceratherium* or *Dicerorhinus* molars, pointing to a high crown.

There does not appear to be any postcranial skeletal material of *Chilotherium* in the East African Miocene collections available to me at present ; Ringström (1924) has established that *Chilotherium* is a brachypothere rhinoceros with the limb and foot bones even more shortened than in *Brachypotherium* (although the metapodials are not so broad at the middle : Ringström 1924 : 58, cf. Table 16), and the excellent Rusinga bones here referred to *Brachypotherium heinzelini.*

To the genus *Chilotherium* Ringström refers forms from the Pontian of Samos and of Maragha, Iran, formerly placed in *Aceratherium* (Ringström 1924 : 83–89), and the genus occurs also in the Vindobonian of Portugal and Spain (Villalta & Crusafont 1955). The earliest occurrence of the genus in Eurasia is in the Burdigalian Bugti Beds of Baluchistan (whence it was originally described as a hippopotamus : Cooper 1934 : 595–596). If the Rusinga and Loperot faunas in which we now have the first evidence of the presence of *Chilotherium* in Africa would be Burdigalian, the appearance of the genus is as early as that in Baluchistan, and earlier than that in Europe.

POSTCRANIAL SKELETON OF *Dicerorhinus* AND *Aceratherium*

There is an abundance of postcranial skeletal material in the East African Miocene collections referable to long-limbed rhinoceroses, including much associated or supposedly associated material. Unfortunately, the extensive literature notwithstanding, our knowledge of the skeleton of the Tertiary rhinoceroses of Europe is far from satisfactory, and in particular the distinction between the limb and foot bones of *Dicerorhinus* and *Aceratherium* is well-nigh impossible. In European collections in which these two genera are represented by cranial or dental material, the identification of unassociated postcranial material is made mainly on the ground of size, a very uncertain guide. At Steinheim, where both *Dicerorhinus germanicus* Wang and *Aceratherium tetradactylum* (Lartet) (as well as the easily recognizable *Brachypotherium brachypus* (Lartet)) occur, the larger bones have usually been ascribed to *Aceratherium*, the smaller to *Dicerorhinus*, in accord with the size of the teeth in the two slender-limbed forms (Fraas 1870 : 203 ; Roger 1900 : 41 ; Wang 1928 : 203). There is a difference, however slight, between *Dicerorhinus* and *Aceratherium*, for *Aceratherium* is tetradactyl, having a fair-sized metacarpal V, whereas in *Dicerorhinus* the fifth metacarpal is reduced. In the living form of *Dicerorhinus*, *D. sumatrensis* (Fischer), metacarpal V is represented by a rudiment, a sesamoid-like bone that, however, has distinct facets for both metacarpal IV and the unciform. Such rudimentary fifth metacarpals have also been found in the Vindobonian *Dicerorhinus caucasicus* Borissiak (1938 : 38) and in Pleistocene *D. hundsheimensis* (Toula 1902 : 47, pl. 8, figs. 1, 6) ; in both cases the rudiment articulates with unciform as well as with metacarpal IV (Toula describes the fifth metacarpal as " das äussere Sesamknöchelchen "). These mammiform bones are hardly longer than their proximal width. On the other hand, in *Aceratherium tetradactylum* metacarpal V is about 80 mm. long, and has a relatively well-developed distal articulation carrying at least two phalanges, although it is narrow proximally and does not bear proximal facets more extensive than those in *Dicerorhinus*. The fifth metacarpal appears to be developed in all aceratheres, such as *Plesiaceratherium gracile* Young (1937) from Shantung, China, *Aceratherium lemanense* (see Duvernoy 1853, pl. 7, fig. 2, as *A. gannatense* ; Repelin 1917, pl. 12, as " *Teleoceras aginense* " (Lavocat 1951 : 114), and Roman 1924 : 51–52, text-figs. 23, 24), *Aceratherium tetradactylum* (Duvernoy 1853, pl. 7, fig. 1 ; Stehlin 1925 : 132, 139), and the terminal *Aceratherium incisivum* (Kaup 1834 : 58, pl. 15, fig. 4 ; 1854, pl. 9 ; 1859). Stehlin (1917) notes that the *Aceratherium* metacarpal V from Sansan (*A. tetradactylum*) is weaker than that in the earlier *A. lemanense*. Professor H. Tobien (private communication) notes that the two skeletons of *Aceratherium incisivum* of the Pontian of Höwenegg (see Tobien 1956) have a metacarpal V in much the same degree of development as in the Aquitanian *Aceratherium lemanense* as figured by Roman (1924 : 51, text-fig. 23). Detailed studies of the Höwenegg skeletons will yield important data that are, however, not yet available at the time of writing.

Thus, in the absence of an associated metacarpal V, the distinction between the hands of *Dicerorhinus* and *Aceratherium* cannot be made. This does not mean that no attempts have been made to establish distinguishing characters in the postcranial skeleton of the two genera, however, but these do not appear to me to have been successful. They will be referred to as we deal with the skeleton in the pages that follow.

The median metacarpals and metatarsals, considered of the greatest value in rhinoceros taxonomy, are remarkably alike in two (cranially and dentally) well-known species such as *Dicerorhinus sansaniensis* and *Aceratherium tetradactylum* of the Vindobonian of Europe, as is evident from the measurements proffered by Pavlow (1892 : 212) as follows (Table 25) :

TABLE 25

Measurements of median metapodials of *Dicerorhinus* and *Aceratherium* (mm.)

	Mc. III		Mt. III	
	length	width	length	width
Dicerorhinus sansaniensis	170	43	150	40
Aceratherium tetradactylum	165	42	153	40

There are no significant proportional differences between these bones. It is futile to insist on the value of such minor differences. The great caution exercised by Stehlin (1925 : 125–139) and Arambourg (1933 : 11) in identifying isolated bones of non-brachypothere rhinoceroses is exemplary, and has, I hope, saved me from drawing conclusions not warranted by the evidence.

Among the associated postcranial material of rhinoceroses from the Miocene of East Africa there is first of all that of two skeletons found in 1947 at R.1, Rusinga. Of these, MacInnes (1951 : 2) writes as follows:

> " The only two complete skeletons yet recovered from the Rusinga deposits have been those of Rhinocerotids. One of these had been exposed on the surface for some considerable time before discovery, and most of the bones were almost weathered away. In the second example, however, the skull, vertebrae, ribs and limbs of the lower side were almost wholly intact and articulated, whilst in the upper half the limbs had been torn off and discarded, though still almost completely articulated, within a few feet of the body. The ribs of the upper side had been forced forwards and backwards from a central point, indicating that the scavengers had penetrated the softer parts of the belly, but had apparently been unable to do any appreciable damage to bones of such bulk. "

In her book *An outline of the geology of Kenya* Mrs. Sonia Cole published a photograph of the two skeletons *in situ* (Cole 1950, pl. 1), showing one skeleton lying on its side with about twelve ribs arranged neatly in their natural position. This is the most conspicuous feature shown in the picture ; the limb and foot bones lie scattered around although some are in articulation, such as a tibio-fibula and a foot near the centre foreground. The skull (or what remained of it) is not shown in the illustration, and apparently had already been removed before the picture was taken. A scapula with the entire spine and tuber spinae is isolated in the right foreground. The specimen in the picture is from the left side, but in the collection it is from the right side, so that the photograph may have been printed back to front. Whether the thorax was lying with its right side up or with the left side up has not been recorded by MacInnes, but in the published picture the twelve or so ribs, which are those of the lower side (we are looking into the emptied thoracic cavity), are from the left side (the vertebral extremities of the ribs are to the right, and the short and wide first rib is foremost in the picture) ; thus, the right side would have been up before removal from the deposit. In the collection the best-preserved ribs of this skeleton are from the right side, those from the left side preserved being fewer in number and rather fragmentary except for the first and last. This is evidence for the distorted side of the thorax (due to penetration by scavengers) having been the left side, which coroborates the conclusion drawn from the scapula that the published photograph has been reversed.

The " de-reversed " picture is given on Pl. 3 of the present paper.

The more complete skeleton of the two from R.1, Rusinga, 1947, belongs to the upper dentition and mandible of *Dicerorhinus leakeyi* bearing no. 2, R.1, 1947, although there are a great many bones that are not numbered (the catalogue of the collection sent from the National Museum indicates that all specimens not otherwise marked are thought to belong to skeleton no. 2, R.1, 1947). In addition, we have the skull remains and mandible marked no. 850 (R.1), 1947, that represent *Aceratherium acutirostratum.* The skeleton belonging to this skull is the one of which MacInnes writes that it had been exposed on the surface for some considerable time, with most of the bones almost weathered away. Some of the bones of this *Aceratherium* skeleton, viz., the scapula sin., the atlas no. 717, and the left radius and ulna no. 850, are in exactly the same state of preservation as those of the no. 2 *Dicerorhinus* skeleton. These bones are fragmented and distorted, the cracks filled with matrix (or plaster occasionally), whitish in colour and evidently preserved in the broken state in which they had been found. There are a number of bones in a different state of preservation, all much deformed and treated with shellac, which gives a brown staining. These bones, thirteen in all, are invariably from the right side (humerus, radius, ulna, scaphoid, lunar, cuneiform, pisiform, femur, patella, tibia and fibula, astragalus, and calcaneum). It is hardly possible to take measurements of these deformed bones, but the radio-ulna is of the same size as the left numbered 850, slightly smaller than that in *D. leakeyi*, and the shellaced right tibia is also slightly shorter than the homologous bone in the no. 2 skeleton of *Dicerorhinus.* These brownish bones I have no doubt should be regarded as belonging to the no. 850 skeleton of *Aceratherium acutirostratum* ; there is no duplication anywhere and the radio-ulnae from both sides agree in size (length). Thus, of the same skeleton we have a few untreated bones from the left side (scapula, radio-ulna) and an atlas, and a great many right bones that have been shellaced.

The picture emerging from these considerations is that of two adult rhinoceros bodies, one (*Dicerorhinus leakeyi*) lying on its right side, the left side of the thorax ripped up by scavengers that tore off some limbs. Of the skull and mandible only the right halves are preserved, the left halves gone. In general, the bones from the right side, more deeply embedded in the sediment, are more complete than the left, although all the larger bones are cracked, distorted and deformed in the course of the fossilization process. The bones of the *Dicerorhinus* skeleton, excluding the smaller elements, are laterally flattened as a result of vertical compression in the fossil deposit. The other body skeleton, slightly smaller and belonging to *Aceratherium acutirostratum*, must have been lying on its left side. The thirteen bones of the right fore and hind limb, still in articulation, had almost weathered away and had to be treated with shellac. The better protected left side of this skeleton, a few bones of which have been saved, could be left untreated.

Here, then, we have two skeletons of different genera, *Dicerorhinus* and *Aceratherium* which would have provided an excellent and rare opportunity to study the intergeneric postcranial skeletal differences, if any, but the state of preservation of the *Aceratherium* bones and many of the *Dicerorhinus* bones is so poor that they are of no use for detailed morphological comparison. We can only state that the *Aceratherium* individual was slightly smaller than the *Dicerorhinus* individual.

To avoid needless repetition of tables and to facilitate comparison I decided not to describe the *Dicerorhinus leakeyi* skeleton of no. 2 separately under its head, and the *Aceratherium acutirostratum* bones of no. 850 apart (nothing of value can be derived from the latter anyway). Instead, I shall deal with all of the postcranial material of non-brachypothere rhinoceroses, including many specimens of uncertain generic position, in the present work bone for bone. But let us first consider the skeleton as a whole.

The skeleton of *Dicerorhinus leakeyi* from Rusinga, relatively complete as it is, provides a welcome opportunity to compare the lengths of the limb segments in one and the same individual with those in the Recent Sumatran species and in Tertiary species from Europe of which an associated skeleton is known. In the literature we find metrical data on the skeleton of the oldest *Dicerorhinus* species known, viz., the small *D. tagicus* Roman (1924) from the Aquitanian of Budenheim, as well as that of *D. caucasicus* Borissiak (1938) from the Vindobonian Chokrak beds in North Caucasus, the former older, the latter younger than *D. leakeyi*. The data are not so complete as may be desired. The skeleton of *D. leakeyi* lacks the metacarpals, and for the length of this segment I have substituted that of an Mc.IV (M.18814), likewise from R.1, to be dealt with later. Although this bone may be *Aceratherium*, it fits well with the bones of *D. leakeyi*. As this is the only complete metacarpal of a slender-limbed rhinoceros in the collection available from these beds I have used Mc.IV of the other skeletons as well. The radius of the *D. leakeyi* skeleton is incomplete; for the length of this limb segment I have used the length of the ulna from the processus anconaeus. The skeleton of *D. tagicus* does not provide more than approximate lengths of ulna and Mc.IV, but those of the remaining limb segments are accurately recorded. Of the skeleton of *D. caucasicus* the lengths of ulna and Mt.III are not known as these bones are incomplete, and the required lengths of humerus and tibia

TABLE 26

Limb segment lengths and ratios in *Dicerorhinus* (mm.)

	D. tagicus	*D. leakeyi*	*D. caucasicus*	*D. sumatrensis*
Length of humerus (greatest)	235	450	*c.* 400	370
Length of ulna (from beak)	*c.* 200	400	—	345
Length of metacarpal IV	*c.* 100	150	137	130
Length of femur (greatest)	305	545	450	423
Length of tibia (greatest)	250	420	*c.* 375	313
Length of metatarsal III	122	180	—	144
Humero-femoral ratio	0·77	0·83	*c.* 0·89	0·87
Ulno-humeral ratio	*c.* 0·85	0·89	—	0·93
Metacarpo-humeral ratio	*c.* 0·43	0·33	*c.* 0·34	0·35
Tibio-femoral ratio	0·82	0·77	*c.* 0·83	0·74
Metatarso-femoral ratio	0·40	0·33	—	0·34

are only approximate. However, the available data lead to some interesting conclusions as to the adaptations to speed and weight in the fossil species. The measurements of *D. sumatrensis* are those of an adult male skeleton from Sumatra in the Leiden Museum (cat. ost. g).

The relative lengths of the limb segments shown by the length ratios in Table 26 differ to a greater or less degree in the four skeletons compared. In the skeleton of *D. leakeyi* the hind limb is less elongated relative to the fore limb than in *D. sumatrensis* ; the ulna is shorter relative to the humerus, but the tibia longer relative to the femur in the Miocene than in the Recent form. The metapodials of both limbs are very nearly equal in length relative to the proximal limb segments in the two skeletons.

In *D. tagicus*, the oldest (Aquitanian) species, the hind limb is still less elongated relative to the fore limb than in *D. leakeyi*, the ulna again shorter relative to the humerus, the tibia still longer relative to the femur ; in all these points the Oligocene skeleton differs more from the Recent than does the Miocene skeleton from Rusinga. But the metapodials, especially of the fore foot, are markedly more elongated relative to the proximal limb segments in *D. tagicus* than in either *D. leakeyi* or *D. sumatrensis*, which differ little in this respect.

The less completely preserved skeleton of *D. caucasicus* shows that the hind limb was probably longer relative to the fore limb than in *D. sumatrensis* ; the metacarpo-humeral ratio is approximately the same as in *D. leakeyi* and *D. sumatrensis*, while the tibio-femoral ratio is about as in *D. tagicus*.

When years ago I compared the Pleistocene skeleton of *Rhinoceros sondaicus* Desmarest from Java with the Recent skeleton of the Javan rhinoceros I found that the Pleistocene skeleton had radius, tibia, and metapodials longer relative to humerus and femur than the Recent, which I interpreted as evidence of the Pleistocene *Rh. sondaicus* having been a more swiftly-moving type, able to make greater speed, than the Recent. The Pleistocene *Rh. sondaicus* is almost identical in limb segment ratios to Recent *Dicerorhinus sumatrensis*, whereas the Recent *Rh. sondaicus* has the skeletal proportions of the Recent Indian rhinoceros, *Rh. unicornis* L. (Hooijer 1946*b*). The intraspecific differences in limb segment ratios found in *Rh. sondaicus* are of the same order of magnitude as those now found between *Dicerorhinus leakeyi* and *D. sumatrensis*.

The Aquitanian species *D. tagicus*, with its long manus and pes, represents a definitely more swiftly-moving type than the Miocene and the Recent species. It is interesting to note, however, that *D. tagicus* appears to be fully tridactyl ; no facet for Mc.V was found on Mc.IV by Roman (1924 : 30). *D. caucasicus*, and probably *D. leakeyi* as well, have a facet for a fifth metacarpal on their Mc.IV, as has the living *D. sumatrensis*. *D. tagicus* is the smallest *Dicerorhinus* known, and has been placed at the beginning of the *Dicerorhinus* " line "(it was unknown to Osborn (1900), who began the line with *D. sansaniensis* of the Vindobonian). The progression into a more slow-moving type along the " line " is shown by the shortened metapodials in the later species. In the relative length of the tibia *D. caucasicus*, although geologically later than *D. leakeyi*, still resembles *D. tagicus* ; the long humerus of

D. caucasicus appears to exceed even that in the living species, however. It is of course probably fortuitous that *D. leakeyi* should have various limb segment ratios intermediate between those of *D. tagicus* and *D. sumatrensis*, and this gradation should not be regarded as evidence for direct phyletic relationship. However limited the value of the above observations may be, I decided not to leave them out as even the slightest information we can derive from a palaeontological find such as the Rusinga skeleton may be needed later when more comparable Tertiary skeletons in Africa or Europe are discovered.

An atlas (no. 717, Rusinga, 1947, thought to belong to no. 850, R.1, Rusinga, the *Aceratherium acutostratum* skeleton) has incomplete wings, and is crushed from above downwards. The dorsal arch shows the two intervertebral foramina the distance between which is 82 mm. (83·5 mm. in the atlas of *Dicerorhinus primaevus* (Arambourg (1959 : 64) ; 51 mm. in *D. sumatrensis*, Leiden Museum, cat. ost. g). The anterior articular cavities for the occipital condyles are relatively well-preserved, and the width across them is 148 mm. (145 mm. in *D. primaevus*, 139 mm. in *D. schleiermacheri* (Kaup 1834 : 41), and 111 mm. in *D. sumatrensis*). The posterior articular surfaces are damaged, but the median ventral tubercle is entire, 15 mm. long and wide, and 20 mm. high. This tubercle, present in the atlas of *D. schleiermacheri* (Kaup 1834, pl. 13, fig. 1) as well as in that of *D. sumatrensis*, Arambourg (1959 : 64) notes to be almost completely effaced in the specimen of *D. primaevus*.

The scapula is represented by a right and left specimen of the same individual, that of the skeleton of *Dicerorhinus leakeyi* no. 2, R.1, Rusinga, 1947. The spine is broken off in the left, but present and nearly entire in the right scapula ; the tuber spinae is a massive process measuring 75 mm. anteroposteriorly (Pl. 11, fig. 1). The portion of the scapula anterior to the spine (supra-spinous fossa) is not completely preserved in either specimen. The thin anterior border is present in the left ; above the neck portion it is nearly straight. The posterior border of the scapula is concave throughout, and thickened in the middle portion. In the right scapula the posterior angle is missing. The glenoid cavity is incomplete costally in the left specimen. Measurements are given in Table 27 below :

TABLE 27

Measurements of scapula of *Dicerorhinus* and *Aceratherium* (mm.)

	Dicerorhinus leakeyi		*Dicerorhinus sumatrensis*	*Aceratherium acutirostratum* sin.
	dext.	sin.		
Height from anterior border of glenoid cavity to upper end of spine	495	505	355	—
Ant. post. diameter above tuber spinae	—	*c.* 270	220	—
Ant. post. diameter of neck	115	115	76	110
Ant. post. diameter over tuber scapulae and glenoid cavity	145	145	105	140
Ant. post. diameter of glenoid cavity	97	97	76	90
Transverse diameter of idem	78	—	60	67
Transverse diameter of tuber scapulae	61	62	32	*c.* 45

The left scapula of the *Aceratherium acutirostratum* skeleton unfortunately is much less complete, lacking the posterior portion above the neck and most of the spine. The glenoid cavity, however, is distinctly smaller than that in the pair of scapulae of the *Dicerorhinus leakeyi* skeleton from the same site. Further, it may be noted that the tuber scapulae is less extended transversely in the *Aceratherium* than in the *Dicerorhinus* specimens. The measurements have been entered in Table 27.

The proximal portion of a left scapula from Rusinga (M.18917, marked Rs.23a) is still less complete; the anteroposterior diameter of the glenoid cavity is 95 mm. Nothing can be said as to its generic position.

In all these scapulae there is a small coracoid process on the costal surface of the tuber scapulae; this process is well developed in a specimen of *Dicerorhinus primaevus* Arambourg (1959 : 64) of which no measurements have been given. Of *D. schleiermacheri* there is a figure of a scapula (Kaup 1834 : 42, pl. 13, fig. 3) with most of the spine missing and incomplete distally. The diameters of the glenoid cavity are given as 79 by 67 mm., smaller than in the specimens of *D. leakeyi*. In *D. sumatrensis* the glenoid cavity is not very much smaller.

Of the humerus we have both the right (Pl. 11, fig. 2) and the left specimen in the skeleton of *Dicerorhinus leakeyi* no. 2, R.1, 1947. Both are fragmented and crushed to a considerable extent. The right is flattened so that the posterior part of the lateral tuberosity is placed very nearly between the caput and the anterior portion of that tuberosity. Half of the caput and all of the medial tuberosity are gone. The posterior surface is not much damaged proximally, but the deltoid tuberosity is missing and the musculo-spiral groove is flattened. Of the distal half of the right humerus only the lateral condyloid crest and the lateral epicondyle are preserved; the trochlea is missing. The left humerus has most of the trochlea, but the proximal half of the bone is crushed and flattened anteroposteriorly, as are the head and the tuberosities except for the anterior part of the lateral tuberosity, which miraculously escaped damage. Nevertheless, a few measurements can be given, all approximate (Table 28).

A poorly preserved right humerus, shellaced and belonging to the skeleton no. 850 of *Aceratherium acutirostratum*, is too much deformed for measurement.

There are also two humerus portions, the proximal portion of a left specimen (M.18915) of which the width over caput and lateral tuberosity is only 125 mm., and the distal half of a left specimen (M.18916) with damaged trochlea and a least shaft width of only 50 mm., greatest distal width 130 mm., of the size of Recent *D. sumatrensis*.

The humerus of *D. schleiermacheri* (Kaup 1834 : 42, pl. 13, fig. 4) appears to agree rather well with those of *D. leakeyi* (the scapula referred to by Kaup (above) is much smaller). The humerus mentioned by Gaudry (1862–67 : 206) to *D. orientalis* is more expanded proximally and distally, and so is that of *D. primaevus* (Arambourg 1959 : 66). The proximal width of a specimen of *D. orientalis* measured by Arambourg (1959) is only 154 mm., however. The trochlea width of the humerus of *D. ringstroemi* is 110 mm. (Bohlin 1946 : 219).

Of two humeri from Steinheim, Roger (1900 : 17) gives measurements entered in Table 28; no. 1 he regards as probably belonging to *Brachypotherium* because of its

TABLE 28

Measurements of humerus of *Dicerorhinus* (mm.)

	D. leakeyi				
	dext.	sin.	*D. schleiermacheri*	*D. orientalis*	*D. primaevus*
Greatest length (laterally)	—	450	457	—	442
Length from caput to medial condyle	—	*c.* 390	—	400	370
Width over caput and posterior part of lateral tuberosity	*c.* 150	—	180	190	191
Width at deltoid tuberosity	—	145+	—	150	156
Least width of shaft	—	*c.* 75	69	—	68
Greatest distal width	—	140+	142	160	167
Width of trochlea	—	*c.* 110	—	—	110

		Steinheim		
	D. sumatrensis	no. 1	no. 2	La Romieu
Greatest length (laterally)	370	420	350	366
Length from caput to medial condyle	337	—	—	—
Width over caput and posterior part of lateral tuberosity	127	140	140	—
Width at deltoid tuberosity	108	—	—	—
Least width of shaft	48	—	—	—
Greatest distal width	115	155	105	103
Width of trochlea	81	110	80	77

greatest distal width (which exceeds the proximal width); no. 2, which would belong to either *Dicerorhinus* or *Aceratherium*, agrees well in comparative slenderness with the humerus from La Romieu referred to *Aceratherium* cf. *platyodon* Mermier by Roman & Viret (1934 : 32, pl. 11, fig. 10).

A left radio-ulna belonging to the skeleton of *Dicerorhinus leakeyi* no. 2, R.1 (Pl. 11, fig. 3) has the ulna nearly entire but the radius incomplete medially and with the distal end shattered. There is no right radio-ulna of the same skeleton in the Rusinga collection sent to me, but there are a right radius and ulna, shellaced and belonging to the skeleton of *Aceratherium acutirostratum* no. 850, R.1, 1947, as well as the untreated left radius (Pl. 9, fig. 2) and ulna marked no. 850, which are slightly smaller than the corresponding bones in *D. leakeyi* (Table 29).

Apart from these associated radio-ulnae there are specifically unidentifiable radii and ulnae. There is a right radio-ulna, laterally flattened and restored with plaster, which is marked R.2 (Rusinga), too badly preserved for measurements to be taken. Then, the proximal part of a right radius (M.18911, marked Rs.21, Rusinga) 97 mm. wide, a proximal end of a left (no number discernible) 83 mm. wide, the distal end of a right radius (M.18910, marked Rs.31, Rusinga) 78 mm. wide, and three distal ends from the left side, M.18914, M.18909, and M.18912, measuring about 75 mm., 80 mm., and 103 mm. in width, respectively.

TABLE 29

Measurements of radius and ulna (mm.)

							Steinheim I		
	D. leakeyi	*A. acutirostratum*	*D. orientalis*	*D. ringstroemi*	*D. primaevus*	*D. sumatrensis*	no. 1	no. 2	no. 3
Radius :									
Median length	355	*c.* 350	330	385	379	293	370	340	315
Proximal width	83	—	70	*c.* 110	105	83	105	87	75
Greatest distal w.	90	—	84	108	102	85	100	90	70

		A. acutirostratum			
	D. leakeyi	dext.	sin.	*D. primaevus*	*D. sumatrensis*
Ulna :					
Greatest length	440	—	—	440	396
Length from processus anconaeus (" beak ")	400	*c.* 395	395	380	345
Length of olecranon (from " beak ")	160	155	—	145	125
Width at semilunar notch	—	—	73	—	69
Middle width	—	—	45	45	39
Greatest distal diameter	67	—	—	67	56

The radius of *D. orientalis* (Gaudry 1862–67 : 206, pl. 32, fig. 4) is somewhat more slender than that of *D. leakeyi* distally ; that of *D. ringstroemi* (Ringström 1924 : 15 ; Bohlin 1946 : 221) on the other hand is wider distally and agrees rather well with the average of five radii of *D. primaevus* given by Arambourg (1959 : 67). The ulna of *D. primaevus* does not differ much in size from those of *Dicerorhinus* and *Aceratherium* from Rusinga, but in one of the *primaevus* ulnae (no. 197) the olecranon is rather short (88 mm.?).

Eight radii from Steinheim (Roger 1900 : 17) vary in length from 295 to 370 mm. and in distal width from 65 to 100 mm. Those with the greatest distal width (100 mm.) Roger regards as probably referable to *Brachypotherium*, but the specimens that have this distal width range in length from 300 to 370 mm. That of which the length is 300 mm. (no. 5 in Roger's table) agrees well with a Rusinga radius that I refer in the present paper to *Brachypotherium heinzelini* (Table 18). The measurements of the largest three Steinheim radii of Roger's are given in Table 29 ; Roger would refer only no. 3 to either *Dicerorhinus* or *Aceratherium*, but nos. 1 and 2 do not differ much in dimensions from those in various fossil *Dicerorhinus* species and may belong to this genus or to *Aceratherium*.

Of the skeleton of *Aceratherium acutirostratum* no. 850, R.1, 1947, we have the three proximal carpals, scaphoid, lunar and cuneiform (Pl. 14, figs. 4, 5) as well as the pisiform from the right side ; these bones were evidently in articulation in the deposit and are much deformed as a whole, fitting well on to each other but inadequate for accurate measurement.

There are three isolated left scaphoids, one from Karungu (M.18897) (Pl. 14, fig. 6), and two marked KB.A, Maboko (= Kiboko) Island (M.18896 and M.18898), and also the anterior portion of a left specimen (M.18899). These bones are similar in proportions and differ only in size; the smallest is even exceeded in size by the scaphoid in *D. sumatrensis* (Table 30).

TABLE 30

Measurements of scaphoid (mm.)

	M.18897	M.18898	M.18896	M.18899	*D. sumatrensis*
Posterior height	71	65	50	—	56
Anterior height	55	49	41	55	55
Proximal width	49	44	38	—	47
Distal width	47	41	37	—	47
Ant. post. at middle	66	58	51	—	65

The Karungu and Maboko Island bones resemble that of *D. schleiermacheri* (Kaup 1834 : 43, pl. 13, fig. 9) in shape except that their posterior height is relatively greater. The proximal projection behind the saddle-shaped radius facet and the distal projection behind the trapezium facet are more developed than in the Eppelsheim specimen, and the height taken over these projections greatly exceeds the height taken in front, over the convexity of the radius facet and the ridge between the facets for trapezium and magnum. Kaup gives neither of these measurements in the text, but from his figures it is clear that the posterior height in *D. schleiermacheri* is only slightly the greater, and so it is in *D. sumatrensis*. Kaup does give the length of the three distal facets (for trapezium, trapezoid, and magnum) as 61 mm., and that of the proximal facets as 49 mm.; these figures agree closely with those in the largest of our scaphoids. The total length of the Eppelsheim bone is given as 90 mm.; the greatest diameter of the Karungu scaphoid, measured over the posterior upper end and the distal outward projection is slightly less (86 mm.). This projection does not extend outward beyond the radius facet, and thus the distal width does not exceed the proximal width, as it does in *Brachypotherium* in contradistinction to *Aceratherium* (and *Dicerorhinus*) (Roger 1900 : 19). The scaphoid of *D. ringstroemi* (Ringström 1924 : 15, fig. 6; Bohlin 1946 : 222, text-fig. 78–2) is much larger than any of our specimens: the greatest diameter is 104 mm., the anterior height 69 mm., although the width of the proximal facet is only 47 mm. Arambourg (1959 : 67) gives measurements of the scaphoid of *D. primaevus*, viz., maximal height 55 mm., and " longueur maxima " (evidently anterposteriorly) 61 mm., which makes the bone intermediate in size between M.18897 and M.18898. The deformed scaphoid of the proximal carpal series of *Aceratherium acutirostratum* (no. 850) is approximately 55 mm. high anteriorly.

One lunar, marked Rs., Rusinga (M.18906), is from the right side and incomplete behind; another, marked R.2, Rusinga (M.18907), from the left side and incomplete medially. Both have a proximal lateral facet for the ulna, as in *Aceratherium* and *Dicerorhinus*, although in M.18906 it is very small. The last-mentioned specimen

(Table 31) closely agrees with the lunar of *D. sumatrensis* in shape as well as size. The anterior height of M.18907 is greater, as in a lunar from Steinheim referred to *Aceratherium* by Roger (1900 : 19). The bone in question of *D. schleiermacheri* is figured only by Kaup (1854, pl. 7) ; that of *D. ringstroemi* is figured by Bohlin (1946 : 223, text-fig. 79–2), with measurements, while that of *D. primaevus* (Arambourg 1959 : 67) is unfigured. The deformed lunar in the associated proximal carpal series of no. 850 (*Aceratherium acutirostratum*) is about 55 mm. high and wide.

TABLE 31

Measurements of lunar (mm.)

	M.18906	M.18907	*D. ringstroemi*	*D. primaevus*	*D. sumatrensis*	Steinheim
Anterior height	40	47	61	—	40	48
Proximal width	45	—	62	50	44	—
Greatest ant. post. diameter	—	68	77	67	65	64

A right cuneiform from Karungu (M.18903), and a left from Rusinga (M.18904), the latter damaged anteriorly below, are rather small, smaller than that in *D. sumatrensis*, but closely similar to it. A left cuneiform from Rusinga (M.25184) is incomplete externally below, and slightly larger. This bone in *D. primaevus* (Arambourg 1959 : 67, " Pyramidal ") is rather extended horizontally. The cuneiform of *Aceratherium acutirostratum* (no. 850) has an anterior height of about 48 mm.

TABLE 32

Measurements of cuneiform (mm.)

	M.18903	M.18904	M.25184	*D. primaevus*	*D. sumatrensis*
Anterior height	38	—	50	46	46
Distal width	32	33	—	—	38
Proximal ant. post. diameter	25	26	32	—	29
Greatest horizontal diameter	36	—	—	50	48

The pisiform is available only in the deformed right carpal series. It is over 60 mm. in length, and at least 40 mm. in distal height (50 mm., and 33 mm. in *D. sumatrensis*). The proximal facets are injured, but one fits well on to the cuneiform.

A right magnum, marked Rs.101, Rusinga (M.18902) is incomplete anteriorly and medially and lacks most of the posterior downward process. A right and a left magnum marked R.3, Rusinga (M.18900 and M.18901), however, are well preserved. The posterior process is much more developed transversely in the right than in the left specimen, *D. sumatrensis* being intermediate in this respect (Table 33) ; *D. primaevus* is unfigured.

Two well-preserved unciforms, one right, marked Rs.31, Rusinga (M.18884), and one left, Kathwanga, Rusinga (M.25191) (Pl. 14, fig. 7) resemble that in *D. sumatrensis*

TABLE 33

Measurements of magnum (mm.)

	M.18902	M.18900	M.18901	*D. primaevus*	*D. sumatrensis*
Greatest anterior height	*c.* 33	25	27	33	30
Greatest anterior width	—	38	36	39	42
Proximal ant. post. diameter	65	53	57	—	67
Greatest diameter	—	82	75	85·5	79

very well indeed. The unciform of *D. schleiermacheri* (Kaup 1834 : 43, pl. 13, fig. 8) is rather small, apparently of a young individual ; those of *D. ringstroemi* (after Bohlin 1946 : 225) present dimensions greater than the Rusinga specimens (Table 34).

TABLE 34

Measurements of unciform (mm.)

	M.18884	M.25191	*D. schleiermacheri*	*D. ringstroemi*		*D. sumatrensis*
Greatest anterior height	45	51	—	—	—	49
Greatest width	60	68	54	*c.* 74	78	61
Greatest ant. post. diameter	80	94	—	105	108	77

In the Rusinga collection there is an entire Mc.IV sin., M.18814, marked R.1, Rusinga, that is associated with the proximal portion of an Mc.III sin., M.18841, with the same inscription. That these bones belong to the same individual cannot be doubted ; their state of preservation is exactly the same and there could not be a better fit (Pl. 12, figs. 2, 3). Then there is the proximal portion of an Mc.II sin. (M.18843) that would seem to belong to the same individual but that is marked Rs., which means that it is a specimen picked up from the surface and not found *in situ* (cf. Le Gros Clark & Leakey 1951 : 3). Its preservation is exactly that of the Mc. III–IV, and size and proximal articulation with Mc.III could not be more fitting.

There is another set of metacarpals from Rusinga representing one or two individuals, and again from the left side. Here are the proximal portions only, that of Mc.II (M.18842) marked Rs. (surface find), but those of Mc.III (M.18837) and Mc.IV (M.18840) marked Rs.31 (Pl. 12, fig. 4). These bones are all incomplete behind, Mc.IV laterally too, and smaller than the set first mentioned.

In both Mc.IV (M.18814 and M.18840) there is a small lateral proximal facet, placed anteriorly, making an obtuse angle with the large proximal unciform facet and only 6–8 mm. wide by an anteroposterior diameter of some 20 mm. There is no posterior interproximal facet on the lateral side of Mc.IV. Now this facet articulated with Mc.IV, but whether this was a mere rudiment or a sizable though small metacarpal it is impossible to tell. As related above (p. 153) *Dicerorhinus* so far as known has a mammiform Mc.V as extended proximally as the short Mc.V in *Aceratherium*, giving the same small facets for articulation with its neighbour and with the unciform (cf. Kaup 1859). Only the find of an Mc.V, associated, would tell the genus to which the other metacarpals belong. Hence, it is uncertain whether the two sets of metacarpals belong to *Dicerorhinus* or to *Aceratherium*, and we have to leave it at that.

Without mentioning these facets, Roger (1900 : 41) writes that the proximal (unciform) facet of Mc.IV in *Aceratherium* is distinctly wider in front, and more rapidly reduces in width posteriorly than that in *Dicerorhinus*, which has a relatively narrower and more anteroposteriorly elongated unciform facet. However, the unciform facet in Recent *D. sumatrensis* Mc.IV is shaped exactly as that in the Rusinga Mc.IV, and of *Aceratherium* I have no reliable material for comparison. The character mentioned as distinctive of the fourth metatarsal of *Aceratherium* by Roger (1900) is found in that of *Dicerorhinus leakeyi* and will be mentioned later on. It seems best to leave the generic position of the metacarpal sets in doubt, although Mc.IV of the larger set fits well with the other bones of *D. leakeyi* as can be seen in Table 26.

There is further an isolated Mc.IV, from the right side (M.18811, Rusinga), that lacks the posterior proximal portion but permits of the median length to be taken (Pl. 12, fig. 1) ; it is more slender than M.18814 but less so than M.18840, and its measurements have likewise been included in Table 35.

The metacarpals of *D. schleiermacheri* are an Mc.III sin. and an Mc.II sin., the latter erroneously described as a right outer (fourth) metacarpal (Kaup 1834 : 43, pl. 13, figs. 13 and 12 ; 1854, pl. 7). The greatest length of Mc.III is given as 204 mm., that of Mc.II as 178 mm. (200 mm., and 177 mm., in Kaup 1854). The median length of the median metacarpal of *D. schleiermacheri* would be some 190–194 mm., 10 mm. less than the greatest length, at any rate exceeding that of *D. primaevus* as given by Arambourg (1959 : 68). The Mc.III of *D. orientalis* (Gaudry 1862–67 : 205/6, pl. 32, fig. 6) has a median length of 164 mm. and a greatest distal width of 61 mm. Of *D. ringstroemi* the left metacarpals III and IV have been made known by Ringström (1924 : 15, fig. 10). The Mc.III has a median length of 187 mm., and a greatest distal width of 68 mm. (even 73 mm. in an incomplete Mc.III). The Mc.IV of *D. ringstroemi* has a median length of 153 mm. and a greatest distal width of 50 mm., measurements that agree very well with those of M.18814. Of *D. primaevus* measurements have been entered in Table 35 ; Mc.IV is shorter and less expanded distally than that of *D. ringstroemi* and the Rusinga specimen, while Mc.III of *D. primaevus* is likewise shorter and less wide distally than that of *D. ringstroemi*. The longest metacarpals are those of *D. schleiermacheri*, and its fourth metacarpal, when known, would probably exceed that of *Dicerorhinus leakeyi* in size. In *D. primaevus* Mc.IV is slightly more shortened relative to Mc.III than in *D. sumatrensis*. It will be observed that the metacarpals of the living species are relatively more expanded distally than those in the Rusinga *Dicerorhinus* or *Aceratherium*. The relative width of the fourth metacarpal in *D. sumatrensis*, however, is exactly the same as that in the Rusinga form.

An Mc.III from Steinheim referred to *Aceratherium* by Roger (1900 : 40) is as long as that of *D. schleiermacheri* : its length is 192 mm. and the middle width 55 mm.

TABLE 35

Measurements of metacarpals (mm.)

Mc.II	M.18843	M.18842	*D. primaevus*	*D. sumatrensis*
Median length	—	—	156	136
Proximal width	43	39	—	35
Proximal ant. post. diameter	*c.* 47	—	—	37
Middle width	*c.* 38	*c.* 33	—	34
Middle ant. post. diameter	—	—	—	18
Greatest distal width	—	—	41	47
Width of distal trochlea	—	—	—	36
Distal ant. post. diameter	—	—	—	41
Mc.III	M.18841	M.18837		
Median length	—	—	179	158
Proximal width	64	49	—	57
Proximal ant. post. diameter	55	*c.* 40	—	47
Middle width	*c.* 50	42	—	45
Middle ant. post. diameter	—	18	—	18
Greatest distal width	—	—	61	59
Width of distal trochlea	—	—	—	48
Distal ant. post. diameter	—	—	—	42
Mc.IV	M.18814	M.18811		
Median length	150	145	140	130
Proximal width	51	41	—	42
Proximal ant. post. diameter	47	—	—	42
Middle width	34	34	—	30
Middle ant. post. diameter	21	21	—	17
Greatest distal width	50	44	38	45
Width of distal trochlea	44	40	—	38
Distal ant. post. diameter	41	37	—	41
Ratio middle width/length	0·23	0·23	—	0·23

Three Steinheim Mc.IV referred to *Aceratherium* by the same author are 150–160 mm. in length, and 30–31 mm. in middle width, very slightly more slender in the shaft than the Rusinga form.

TABLE 36

Measurements of metacarpals (mm.)

	M.18845	M.18848	K.4, 1950	M.18838	M.18839	M.18851	M.25183
Proximal width	41	39	41	55	58	53	48
Proximal ant. post. diameter	—	—	—	42	50	46	45

In addition to the above-mentioned metacarpals there are various proximal metacarpal portions that belong either to *Dicerorhinus* or to *Aceratherium*, viz.,

M.18845, Rusinga, Mc.II sin., damaged behind,
M.18848, Kachuku, Lower Series, Karungu, Mc.II dext., incomplete behind,
K.4, 1950, Ngira, Karungu, Mc.II sin., articular surface incomplete,

M.18838, Rusinga, Mc.III dext.,
M.18839, Rs.103, Rusinga, Mc.III dext.,
M.18851, Kachuku, Lower Series, Karungu, Mc.III sin., and
M.25183, Rusinga, Mc.III sin.

Four phalanges are unnumbered and associated ; they are thought to belong to the skeleton of *Dicerorhinus leakeyi* no. 2, R.1, 1947. They comprise the first and second phalanges of the median digit and of a lateral digit, and if they belong to the no. 2 skeleton they form part of the fore foot as the median phalanges of both hind feet of the skeleton are present. Measurements are given in Table 37.

TABLE 37

Measurements of anterior phalanges (mm.)

	Rusinga		*D. primaevus*		*D. sumatrensis*		
	median digit	lateral digit	median digit	lateral digit	II	III	IV
Phalanx I, length	36	37	39	42	34	33	31
Proximal width	50	*c.* 41	55.	39·5	39	48	40
Phalanx II, length	26	25	27	28	23	26	23
Proximal width	53	39	55	40	34	52	35

There is a considerable number of fragments of ribs, some annotated, some not, all belonging to the skeleton of *Dicerorhinus leakeyi* no. 2, R.1, 1947. Encouraged by the photograph published by Cole (1950, pl. 1), which shows that at least the ribs of one side had been mostly there in a complete state, I have tried to reassemble the fragments, and arrange them, after determining the side to which the ribs belong (possible in most cases), in such a way as to obtain a graded series. The head and tubercle, the relative size and position of which gradually change as one passes along the series, are only rarely available, but using Recent rhinoceros skeletons of various genera (*Diceros*, *Rhinoceros*, and *Dicerorhinus*) in the Leiden Museum as a guide, it has been possible to determine all but a few of the twenty right ribs that were on the lower side of the skeleton before excavation, and about half that number of left ribs. The numbering of the fossil ribs is, of course, to some extent provisional.

To begin with, the ribs, and especially the wide anterior ribs up to about the ninth, are distorted, as are most of the larger bones of this skeleton. In some of the ribs, when laid with their posterior border on a table, the body does not stand up but is nearly flat on the table. The sternal ends are better preserved than the vertebral.

The first rib, easily recognizable because of its large tubercle, shortness, and rapid increase in greatest diameter toward the sternal end, is present from both sides. The left rib is best preserved, the head only being lost. The lateral flattening and distortion (there is a peculiar S-twist near the middle of the body that is unnatural) are severe, however. Its greatest length is 280 mm., the maximal diameter at the sternal end 50 mm., while at the narrowest point below the (missing) head it measures 28 mm. anteroposteriorly and 17 mm. transversely in cross section. In the right first rib both extremities have been lost ; the cross section as taken on the left rib is 22 by

20 mm., showing that the right rib is less laterally compressed than the left. In an adult male of *D. sumatrensis* used for comparison with the fossil skeleton throughout the first rib is 230 mm. long, 33 mm. in greatest sternal diameter, and 20 by 13 mm. in section below the head.

The second rib, from the right side, is a slightly curved specimen without head or tubercle but with the sternal end. Length as preserved 380 mm. (the length of the complete second rib in *D. sumatrensis*), and greatest diameter at middle of body 40 mm. (24 mm. in *D. sumatrensis*). Of the left second rib the proximal portion only is present in the collection.

The head and tubercle are preserved in the anterior of two right ribs that are still held together by matrix proximally. They agree best with the third rib in Recent skeletons in the configuration of the vertebral end. The third rib, then, is incomplete sternally ; length 490 + mm. (440 mm. in *D. sumatrensis*), and greatest diameter at middle 36 mm. (26 mm.). The fourth right rib, the sternal end of which is preserved, had a length of about 600 mm. (520 mm.) when complete, by a greatest diameter at middle of about 50 mm. (29 mm.).

The (?) fifth right rib lacks a portion of the body that I have been unable to find among the fragments ; diameter at middle of about 50 mm. (32 mm.). The (?) sixth right rib which has the sternal end but no head, is 530 mm. long as preserved, and 52 mm. (30 mm.) in greatest middle diameter. The (?) seventh right rib is without the vertebral end, a body fragment only 275 mm. long and 49 mm. in greater diameter.

What is probably the sixth or seventh left rib is an entire specimen, 750 mm. long along the curve, and 50 mm. in diameter along most of its length. In *D. sumatrensis* the sixth and seventh ribs are 630–670 mm. long and 27–30 mm. in diameter.

The (?) eighth right rib is entire, with a length of 900 mm. (700 mm.) and a greatest diameter of 42 mm. (22 mm.).

A number of right ribs, all without the vertebral end, have the same curvature as the (?) eighth, and either the same or a smaller thickness. These I have arranged so that the sternal end decreases in size posteriorly. The best preserved is the (?) eleventh rib, of which the costal tubercle at least (already much reduced) is present. The total length is probably 900 mm. (730 mm.) and the greatest diameter 34 mm. (23 mm.).

From the eleventh rib onwards the ribs in Recent species become very thin mediolaterally (least so in *Rhinoceros*), whereas the fossil ribs assigned to this region are more robust. The curvature remains the same until the seventeenth rib has been reached. We have the greater part of what appear to be the twelfth to seventeenth ribs from the right side, and fragments of the ninth to thirteenth ribs from the left side, the side into which the scavengers penetrated. The greatest diameters of the incomplete specimens vary from 30 to 37 mm. (21–26 mm. in *D. sumatrensis*). The almost entirely preserved (?) eleventh rib must have been one of the longest, as in the Recent species the length starts to decrease backward from about the eleventh rib.

The penultimate and last ribs are very thin at their free end, which are preserved in what appear to be the eighteenth, nineteenth, and twentieth ribs from the right side. But the last rib (twentieth?) from the left side even has the vertebral end too, in which tubercle and head have become united. Its length along the curve is 410 mm., the greatest vertebral diameter 39 mm., at the free end 10 mm. In *D. sumatrensis* the twentieth rib is absent although the nineteenth is still 420 mm. long. In *Diceros bicornis* (L.) one skeleton (Leiden Museum reg. no. 5738) has the twentieth and last rib with the same diameters at the ends as in the fossil, but its length is only 280 mm.

Of the pelvis of the skeleton of *Dicerorhinus leakeyi* no. 2, R.1, 1947, there is only a portion from the right side, which shows the acetabulum, part of the shaft of the ilium, and the pubis and ischium around the obturator foramen, but the specimen is fragmented and distorted to such a degree that no measurements can be recorded.

The left femur is one of the best preserved bones of the skeleton of *D. leakeyi* no. 2, R.1, 1947. Its distal part is slightly displaced relative to the proximal portion, but the usual flattening is not extensive (Pl. 13, fig. 1). The right femur of the same individual has the distal end crushed and incomplete, and the proximal end missing. It has, however, the (flattened) third trochanter, broken off in the left specimen. Measurements are recorded in Table 38.

TABLE 38

Measurements of femur of *Dicerorhinus* and *Aceratherium* (mm.)

			D. orientalis (Pikermi)				
	D. leakeyi sin.	*D. schleiermacheri*	(Gaudry)	(Arambourg)		*D. ringstroemi*	*D. primaevus*
Greatest length	545	555	540	491	499	—	538
Proximal width	215	—	—	192	198	—	223
Least width of shaft	75	—	90	75	75	—	82
Greatest distal width	*c.* 145	153	155	145	146	170	150
Distal ant. post. diameter, medial side	180	160	—	—	—	*c.* 235	—
Transverse diameter caput	95	—	—	—	—	—	—

		Steinheim (Roger 1900)				
	D. sumatrensis	no. 1	no. 2	no. 3	no. 5	*Aceratherium incisivum*
Greatest length	423	540	533	450	395	—
Proximal width	162	—	—	—	—	—
Least width of shaft	56	—	—	—	—	—
Greatest distal width	125	150	138	110	105	123
Distal ant. post. diameter, medial side	150	—	—	—	—	149
Transverse diameter caput	73	—	—	—	—	—

The right, shellaced femur of the skeleton of *Aceratherium acutirostratum* no. 850, R.1, 1947, consists of the proximal and distal portions that do not fit, and the deformation does not permit of measurements to be taken. There is also the isolated caput of a femur, no. 991, Rusinga, 1947, that measures 79 mm. transversely, almost as small as in *D. sumatrensis*.

The femur of *D. leakeyi* agrees very well in size with the largest femur of *D. primaevus* (Arambourg 1959 : 70) given in the Table; that of *D. schleiermacheri* (Kaup 1834 : 44, pl. 13, fig. 5) is longer than either of them. The femur of the Pikermi *D. orientalis* as given by Gaudry (1862–67, pl. 32, fig. 7) is rather similar, but the femora recorded by Arambourg (1959 : 70) as belonging to the same species are noticeably shorter. The bone in *D. ringstroemi* (Bohlin 1946 : 227) is wider distally than any of the others presented in Table 38. Of the Steinheim femora recorded by Roger (1900 : 17) the largest (no. 1) is like that of *D. leakeyi* in the few measurements given. Roger would refer most of the Steinheim femora to *Brachypotherium* except the slender (and short) no. 5, which he would place with *Aceratherium.* The femur referred to *Aceratherium incisivum* by Kaup (1834 : 59, pl. 15, fig. 1) has a greater distal width than Roger's nos. 3 and 5, but its length is unknown. The *Aceratherium* (or *Dicerorhinus*?) femur agrees with that of *D. sumatrensis* in size.

The patella is represented by five specimens. No. 718, which belongs to the skeleton of *Dicerorhinus leakeyi* no. 2, R.1, 1947, is corroded, rather small, and drawn out in a point distally. There are a large right specimen belonging to the skeleton of *Aceratherium acutirostratum* no. 850, distorted and incomplete, and three unnumbered specimens, one left and two right, the last of which bears the mark Rs.31, Rusinga.

TABLE 39

Measurements of patella (mm.)

	D. leakeyi dext.	*A. acuti-rostratum*	sin.	dext.	dext. Rs.31	*D. sumatrensis*
Length	76+	—	84	98	105	91
Width	60+	85	83	87	82	77

It may seem peculiar that the patella of the *Dicerorhinus* from Rusinga (it fits well on to the articular surface of the right femur, and certainly belongs to the no. 2 skeleton) is so much smaller than that of the *Aceratherium*, whereas in the other bones of the two skeletons *D. leakeyi* is (slightly) the larger as far as can be seen. The patella, however, may be just abnormally stunted in the *D. leakeyi* skeleton; it is unfortunate that we do not have this bone from the left limb also.

The patella of *D. schleiermacheri* (Kaup 1834 : 44, pl. 13, fig. 7) differs from that referred to *Aceratherium incisivum* (Kaup 1834 : 60, pl. 15, fig. 12) in being more squarish; that of *A. incisivum* (it should be noted that it has been figured upside down) is more drawn out medially. The length is 90 mm. in both; the width about 80 mm. in *D. schleiermacheri* against 94 mm. in *A. incisivum.*

A left tibia and fibula (Pl. 13, fig. 2) but only the right fibula, are labelled as belonging to the skeleton no. 2, R.1, 1947; *Dicerorhinus leakeyi.* The tibia is somewhat laterally flattened in its proximal part, but the distal end is well-preserved. Fortunately the right tibia of the shellaced limb of *Aceratherium acutirostratum,* though laterally flattened, permits a few measurements to be taken, which show it to be slightly shorter than that of *D. leakeyi* (Table 40). A right tibia marked KB.S, Maboko (= Kiboko) Island, lacks the lateral proximal portion. The proximal portion of a right tibia (M.18920), marked Rs.105, Rusinga, the lower two-thirds of a right tibia marked R.1, Rusinga, the distal end of a right tibia (M.18919) marked Rs.31, Rusinga, and that of a left tibia (M.18918) marked Rs., Rusinga, are the remaining specimens in the collection ; measurements so far as possible are recorded in Table 40.

TABLE 40

Measurements of tibia of *Dicerorhinus* and *Aceratherium* (mm.)

	D. leakeyi sin.	*A. acuti-rostratum*	KB.S	M.18920	R.1	M.18919	M.18918
Greatest length	420	*c.* 410	380	—	—	—	—
Medial length	375	*c.* 370	350	—	—	—	—
Proximal width	—	—	—	125+	—	—	—
Distal width	100	—	82	—	95	92	95
Distal ant. post. diameter	*c.* 80	—	79	—	*c.*80	73	72

	D. schleier-macheri	*D. orientalis*	*D. primaevus*	*D. sumatrensis*	Steinheim no. 1	Steinheim no. 2
Greatest length	388	—	—	313	340	300
Medial length	—	350	340–372	282	—	—
Proximal width	130	126	119–130	116	110	120
Distal width	—	96	98–109	82	75	100
Distal ant. post. diameter	68	—	—	59	—	—

The tibia of *D. schleiermacheri* has a greatest length less than that in *D. leakeyi* (taken from Kaup 1854 ; the other measurements after Kaup 1834 : 44). That of *D. orientalis* (Gaudry 1862–67 : 207, pl. 32, fig. 8) is within the limits of eleven (!) tibiae of *D. primaevus* (Arambourg 1959 : 71) or nearly so. Of the Steinheim tibiae recorded by Roger (1900 : 18) no. 1 is regarded as representing *Aceratherium*, the shorter one (no. 2) is as short as in *Brachypotherium* but not quite so broad ; in *Brachypotherium brachypus* the proximal width is one-half the length.

The fibula belonging to the skeleton of *Dicerorhinus leakeyi* no. 2, R.1, 1947, is longer than the three fibulae recorded from Steinheim by Roger (1900 : 18). Of these, that with a length of 280 mm. (see Table 41) is stated to belong to the supposed *Aceratherium* tibia that is 340 mm. in greatest length (Steinheim no. 1 in Table 40) ; the others must have belonged to even longer tibiae. The preservation of the right fibula of the skeleton of *D. leakeyi* is perfect ; it is an enigma to me why the right tibia of the skeleton has not been preserved.

There is an abundance of astragali in the present East African collection : some twenty specimens in all one of which (no. 538, Gumba, Rusinga, 1949) is that of *Brachypotherium* and is dealt with under the head *B. heinzelini* in the present paper. All the others belong to either *Dicerorhinus* or *Aceratherium*.

TABLE 41

Measurements of fibula of *Dicerorhinus* and *Aceratherium* (mm.)

	D. leakeyi dext.	*D. sumatrensis*	Steinheim		
Length	350	275	280	332	320
Greatest proximal diameter	45	42	—	—	—
Greatest distal diameter	47	39	—	—	—

The following specimens are from the right side :

1. M.18875, Rs., Rusinga.
2. No. 132, R.2–4, Rusinga, 1949.
3. F.3264, R.4, Rusinga, 1942.
4. M.18881, Rs.38, Rusinga.
5. No. 679, R.106, Rusinga, 1947.
6. M.18876, Karungu.
7. M.18878, Karungu.
8. M.18882, KB.A, Maboko (= Kiboko) Island.
9. K.382, 1950, Ngira, Karungu.
10. The deformed specimen of the limb of *Aceratherium acutirostratum.*

Those from the left side are as follows :

11. No. 2, R.1, 1947, of the skeleton of *Dicerorhinus leakeyi* (Pl. 14, fig. 1).
12. M.18880, Rs., Rusinga.
13. Arongo Chianda, 25.x.1939.
14. M.18877, Rs.21, Rusinga.
15. M.18879, Rs.31, Rusinga.
16. Aloir '39, Owen (Pl. 14, fig. 2).
17. No. 528, Kiune, Rusinga, 1949.
18. M.18883, Rs., Rusinga.
19. No. 1054, S.E. of Kiahera Hill, Rusinga.

Most of the specimens are to some extent damaged, and often the lateral trochlea ridge is incomplete. This is also the case in the astragalus of the *Dicerorhinus leakeyi* skeleton, but in this case the associated calcaneum is preserved and fits on to it perfectly (Pl. 14, fig. 1) so that the lateral height (over the top of the lateral trochlea ridge and the lateral edge of the distal cuboid facet) can be exactly determined. The medial height of the astragalus, which can be almost invariably taken (over the medial trochlea ridge and the distal navicular facet), is usually slightly less than the lateral height. The difference is apparently of no significance, but it has been cited (Wang 1928 : 204) as constituting a probable means of distinction between *Dicerorhinus* and *Aceratherium.* Wang observed that in *Aceratherium* the astragalus would be higher laterally than medially, whereas in *Dicerorhinus* lateral and medial height would be equal, or the medial height greater than the lateral. Now, as will be seen from Table 42, in four out of the ten astragali of which both the lateral and the medial height are known the lateral slightly exceeds the medial height, including that (no. 11) of *D. leakeyi,* which thereby would present the *Aceratherium* character.

Further, the astragalus from Viehhausen associated with a dentition of *Aceratherium tetradactylum* as recorded by Rinnert (1956 : 33, pl. 3, figs. 1, 3) appears to be equally high on both sides, and thereby *Dicerorhinus*-like. Therefore, it seems to me that reliable distinguishing characters for *Dicerorhinus* on the one hand, and *Aceratherium* on the other, are still to be found.

TABLE 42

Measurements of astragalus of *Dicerorhinus* and *Aceratherium* (mm.)

No. of specimen	1	2	3	4	5	6	7	8	9
Lateral height	66	—	81	67	67	—	—	70	—
Medial height	67	71	78	66	71	72	72	72	73
Total width	71	88	89	81	73	85	86	83	80
Ratio medial height/ total width	0·94	0·81	0·88	0·81	0·97	0·85	0·84	0·87	0·90
Trochlea width	64	69	78	65	65	67	72	66	67
Width of distal facets	69	75	76	73	66	78	71	72	73

No. of specimen	11	12	13	14	15	16	17	18	19
Lateral height	90	63	—	—	—	88	71	71	—
Medial height	88	67	70	69	73	85	72	72	65
Total width	97	84	—	81	—	96	85	84	—
Ratio medial height/ total width	0·91	0·80	—	0·85	—	0·89	0·85	0·86	—
Trochlea width	86	67	70	68	70	84	72	69	—
Width of distal facets	82	73	73	69	—	77	75	—	—

In the East African specimens the trochlea width (measured over the lateral and medial surfaces) is either less than the medial height or equal to it (in *Brachypotherium* the trochlea width exceeds the medial height). The total width (measured over the medial distal tuberosity and the lateral edge of the trochlea) does not exceed the medial height to the extent seen in *Brachypotherium* (Table 19) ; the ratio of medial height to total width varies in fifteen specimens from 0·80 to 0·97, as opposed to 0·73 or less in *Brachypotherium*.

The astragalus of *D. schleiermacheri* (Kaup 1834 : 45, pl. 13, fig. 11) is a rather high specimen, the lateral height being given as 85 mm., the trochlea width as 70 mm., and the greatest width as 81 mm. From Kaup's illustrations it seems that the external height has been taken over the ridge between the cuboid and the navicular facet, and that the trochlea width has not been taken over the lateral and medial surfaces but perhaps at the top of the ridges. In the British Museum (Natural History) there is a cast of a right astragalus from Hessen-Darmstadt, M.2786, catalogued as being of the specimen figured by Kaup (1834, pl. 13, fig. 11) as *D. schleiermacheri*. Its measurements are given in Table 43 ; they correspond well with those of the East African astragali although the trochlea width exceeds the medial height. The astragalus of *D. ringstroemi* (Ringström 1924 : 16, text-fig. 8) is larger than the largest Rusinga specimen ; that of *D. primaevus* (Arambourg 1959:

72) in the few measurements given seems to agree well with our no. 3 (F.3264, from Rusinga). Under *Aceratherium incisivum* Kaup (1834, pl. 15, fig. 2) figures an astragalus from Oppenheim[1] that is relatively much higher than an astragalus from Budenheim (pl. 15, fig. 10). According to the measurements given by Kaup (p. 60) the trochlea width (stated to have been taken over the external and internal surfaces) much exceeds the medial height in the Budenheim specimen, although it evidently does not have the great total width characteristic of *Brachypotherium*. An astragalus from Steinheim recorded by Roger (1900 : 24) as *Aceratherium* is rather high laterally (perhaps measured over the distal ridge between cuboid and navicular facets), but the ratio of medial height to total width is as in various Karungu and Rusinga specimens. The astragalus associated with teeth of *Aceratherium tetradactylum* (Rinnert 1956 : 34, pl. 3, figs. 1, 3) is intermediate between the two *Aceratherium* specimens figured by Kaup in medial height as well as in trochlea width. The one and only definite *Aceratherium* astragalus in our collection (no. 10) cannot be measured because of its poor state of preservation. That from Losodok cautiously identified by Arambourg (1933 : 10) as *Aceratherium*? sp. corresponds with various of our specimens in height and total width (74, and 86 mm., respectively) and, as Arambourg realized, represents either *Aceratherium* or *Dicerorhinus*.

TABLE 43

Measurements of astragalus of *Dicerorhinus* and *Aceratherium* (mm.)

	D. schleiermacheri	*D. ringstroemi*	*D. primaevus*	*D. sumatrensis*	Oppenheim	Budenheim	Viehhausen	Steinheim
Lateral height	—	—	—	66	63	71	—	76
Medial height	75	—	79	68	61	67	64	66
Total width	93	100	90	82	—	—	—	78
Ratio medial height/ total width	0·81	—	0·88	0·83	—	—	—	0·85
Trochlea width	80	89	—	70	63	77	67	—
Width of distal facets tuber	76	—	—	66	68	66	—	—

In sharp contrast to the abundance of astragali, there are only three specimens of the calcaneum in the East African Miocene collection, the left calcaneum of the skeleton of *Dicerorhinus leakeyi* no. 2, R.1, 1947, well preserved (Pl. 14, fig. 1), a much deformed shellaced specimen belonging to the right limb of *Aceratherium acutirostratum*, and no. 679, R.106, Rusinga, 1947. The last is from the left side but evidently is of the same individual as the right astragalus bearing the same number (no. 5 in Table 42). The tuber and the cuboid facet are not complete, and approximate measurements only can be given.

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[1] The Oppenheim astragalus has the medial and the distal calcaneum facets confluent, which is regarded as typical for *Aceratherium* by Ringström (1924 : 74, text-fig. 43). In the Budenheim astragalus these two facets are separate. The difference is apparently trivial ; there may, or may not, be a shallow non-articular groove between these two facets. In most of the East African astragali the junction area of the medial and distal calcaneum facets is damaged, but in M.18881 and M.18882 the two facets are confluent, in no. 679 separate, whereas in the astragalus of *D. leakeyi* there appears to be a very narrow groove between the two, an intermediate condition we see also in *D. sumatrensis*. In two astragali from Steinheim figured by Fraas (1870 : 302, pl. 7, figs. 7, 8) as *Rh. sansaniensis* and *Rh. brachypus* (that is, *Dicerorhinus* and *Brachypotherium*) respectively, the medial and distal calcaneum facets are separate. The larger specimen (pl. 7, fig. 8) agrees in shape and size with *Aceratherium tetradactylum*, while the smaller (pl. 7, fig. 7) may belong to *Dicerorhinus* (Rinnert 1956 : 36). Needless to say, I do not think that the presence or absence of a bridge between the medial and the distal calcaneum facet of an astragalus is more than an individual variation, useless for intergeneric comparison.

TABLE 44

Measurements of calcaneum of *Dicerorhinus* and *Aceratherium* (mm.)

	D. leakeyi		*D. schleiermacheri*	*D. primaevus*	*D. sumatrensis*	Budenheim	Viehhausen	Steinheim
	sin.	no. 679						
Lateral height	148	—	135	132	106	122	110	129
Greatest width	89	*c.* 60	—	76	71	—	71	82
Ant. post. cuboid facet	48	*c.* 40	48	—	39	48	—	—
Transv. cuboid facet	*c.* 25	—	24	—	23	21	—	—
Greatest diameter tuber	73	*c.* 60	71	—	63	81	57	—
Transv. diameter tuber	54	—	52	—	46	45	—	46

The calcaneum of *D. schleiermacheri* (Kaup 1834 : 45, pl. 13, fig. 10) appears to correspond well with that of *D. leakeyi*; the Rusinga bone is only somewhat longer. The greatest width of the Eppelsheim specimen is about 80 mm. That of *D. primaevus*, the length and width only of which are known, is smaller though it is near to the calcaneum from Steinheim recorded by Roger (1900 : 23) (which is perhaps the same as the specimen figured by Fraas 1870, pl. 7, fig. 10). The bone in question, figured as *Rh. sansaniensis* (hence, *Dicerorhinus*), is considered indistinguishable from that of *Aceratherium tetradactylum* by Rinnert (1956 : 36). The Budenheim calcaneum ascribed to *Aceratherium incisivum* (Kaup 1834 : 60, pl. 15, fig. 11) differs from that of *A. tetradactylum* from Viehhausen figured by Rinnert (1956, pl. 3, figs. 1, 2) only in size and the configuration of the tuber.

Of the skeleton of *Dicerorhinus leakeyi* no. 2, R.1, 1947, we have the entire left navicular, and also an anterior fragment of the right (separately catalogued under no. 360). There are also two right and two left naviculars, viz.,

M.18887, R.1, Rusinga,
M.25187, Kathwanga, Rusinga, 1947,
No. 64, 1950, R.1, Rusinga, and
M.25188, Kathwanga, Rusinga, 1947.

These bones are very similar in shape and differ mainly in dimensions; the navicular of *D. sumatrensis* is only relatively wider (the width of these bones has not been recorded for *D. ringstroemi* (Ringström 1924 : 16, text-fig. 8) or for *D. primaevus*). The navicular of *D. schleiermacheri* (Kaup 1834 : 45) is larger than that in *Aceratherium incisivum* (Kaup 1834: 60, pl. 15, fig. 9*a*–*c*), which is similar in size to that of the recent species; its total width is about 50 mm.

TABLE 45

Measurements of navicular of *Dicerorhinus* and *Aceratherium* (mm.)

	D. leakeyi	M.18887	M.25187	no. 64	M.25188	*D. primaevus*
Greatest anterior height	31	31	26	25	20	30
Total width	49	52	47	47	44	—
Ant. post. diameter	69	71	60	64	54	60

	D. ringstroemi	*D. sumatrensis*	*Aceratherium incisivum*
Greatest anterior height	27	20	—
Total width	—	50	—
Ant. post. diameter	75	54	56

There is the left cuboid of the skeleton of *Dicerorhinus leakeyi* no. 2, R.1, 1947 (Pl. 13, figs. 4, 5) and in addition no less than eight isolated cuboids, six right and two left :

M.18892, Karungu,
M.18890, R.1, Rusinga (Pl. 13, fig. 6),
M.18891, Kachuku, Lower Series, Karungu,
No. 440, Ngira, Karungu,
M.18894, Rs.105, Rusinga,
M.18893, R.8, Rusinga,
M.18895, Kachuku, Karungu, and
M.18889, Rs., Rusinga.

These cuboids appear to fall into two groups, viz., one in which the anterior height is nearly equal to the anterior width, and one (M.18890 and M.18893) in which the anterior surface is distinctly higher than wide (Table 46). In *Brachypotherium* the cuboid is distinctly wider than high anteriorly (Roger 1900 : 24) ; the present specimens represent either *Dicerorhinus* or *Aceratherium*. In *D. schleiermacheri* the anterior height of the cuboid is equal to the anterior width (Kaup 1834 : 45), and so it

TABLE 46

Measurements of cuboid of *Dicerorhinus* and *Aceratherium* (mm.)

	D. leakeyi	M.18892	M.18890	M.18891	no. 440	M.18894	M.18893
Anterior height	48	48	46	42	41	41	36
Anterior width	47	47	36	43	42	40	30
Greatest ant. post. diameter	64	73	63	69	—	*c.* 65	66

					Aceratherium	
	M.18895	M.18889	*D. primaevus*	*D. sumatrensis*	(Roger)	(Rinnert)
Anterior height	40	34	48	40	46	40
Anterior width	37	35	39	40	34	30
Greatest ant. post. diameter	—	—	—	56	—	—

is in the cuboid of *D. leakeyi* and in that of Recent *D. sumatrensis*. However, the cuboid of *D. primaevus* as appears both from the measurements and from the illustration (Arambourg 1959 : 72, text-fig. 32B) is decidedly higher than wide. This is also the case in the Steinheim *Aceratherium* recorded by Roger (1900 : 24) and in *Aceratherium tetradactylum* from Viehhausen (Rinnert 1956 : 34, pl. 3, fig. 1). In *A. incisivum* (Kaup 1834 : 45, pl. 15, fig. 9) the anterior width of the cuboid appears to be somewhat greater than the height. Therefore, it would seem that the relative height of the cuboid cannot be used in intergeneric differentiation.

Both ectocuneiforms of the skeleton of *Dicerorhinus leakeyi* no. 2, R.1, 1947, are available. There are four other ectocuneiforms, all from the right side :

M.18905, R.1, Rusinga,
M.18886, Rs.105, Rusinga,
M.18885, Rs.30, Rusinga, and
M.18888, Rs., Rusinga.

Of these, M.18905 fits on to the navicular M.18887, and belongs to the same individual. It is higher, but not wider than the ectocuneiform of *D. leakeyi* (Table 47). The ectocuneiform of *D. sumatrensis* is less elongated anteroposteriorly than the fossil bones. That of *D. primaevus* (Arambourg 1959 : 72) appears to be rather low ; the width, given as 23 mm., is omitted in the Table as it is probably a misprint (53?).

TABLE 47

Measurements of ectocuneiform of *Dicerorhinus* and *Aceratherium* (mm.)

	D. leakeyi	M.18905	M.18886	M.18885	M.18888	*D. primaevus*	*D. sumatrensis*
Anterior height	27	31	26	26	25	21·5	24
Anterior width	55	51	50	44	43	—	47
Ant. post. diameter	53	51	52	50	48	60	43

Only the right mesocuneiform of the skeleton of *Dicerorhinus leakeyi* no. 2, R.1, 1947, has been saved. It is more elongated anteroposteriorly than that in *D. sumatrensis* (Table 48).

TABLE 48

Measurements of mesocuneiform of *Dicerorhinus* (mm.)

	D. leakeyi	*D. primaevus*	*D. sumatrensis*
Height	19	21	16
Width	22	26	19
Ant. post. diameter	41	—	29

The left entocuneiform only of the skeleton of *Dicerorhinus leakeyi* no. 2, R.1, 1947, is available ; the proximal portion articulating with navicular and mesocuneiform has broken off, and only the facet for Mt.II remains. The posterior tuberosity is much larger than that in the entocuneiform of *D. sumatrensis* (in parentheses) : height 47 mm. (27 mm.), and width 30 mm. (22 mm.).

All the metatarsals from the left side, as well as the Mt.II and IV from the right side of the skeleton of *Dicerorhinus leakeyi* no. 2, R.1, 1947, are preserved (Pl. 13, fig. 3 ; Pl. 15). No other entire metatarsals are in the East African Miocene collection. Roger (1900 : 41) has tried to separate the metatarsal IV of *Dicerorhinus* from that of *Aceratherium*, and states that Mt.IV in *Aceratherium* has a postero-lateral incurvation of the large proximal cuboid facet, which makes this facet trilobate or trefoil-shaped, with the shaft forming a prominence behind the incurvation, whereas in Mt.IV of *Dicerorhinus* the cuboid facet is distinctly narrower and more antero-posteriorly elongated. My observations do not bear this out ; on the contrary the cuboid facet on Mt. IV in *Dicerorhinus sumatrensis* and that in *D. leakeyi* answer to the description of the facet of Roger's *Aceratherium*, and the cuboid facet of Mt.IV of *Aceratherium tetradactylum* associated with the dentition at Viehhausen is described by Rinnert (1956 : 34) as broadly elliptical.

The right second metatarsal of the *D. leakeyi* skeleton shows an interesting pathological condition (Pl. 15, figs. 1–3). The distal half is thickened, and the distal articulation wholly deformed. The swollen surface shows irregular growths all over and appears spongy. Without radiological or histological examination the attribution of such an affection of the bone to a specific disease is impossible, but the outward appearance of the fossil is suggestive of something like Paget's disease. No other bones of the skeleton (nor the skull so far as preserved) appear to be afflicted with this disease (which may occur quite localized in the human skeleton) ; it may have developed of course in some of the missing elements like the metacarpals or the right tibia. The phalanges of this digit were certainly affected, but these are not present in the collection.

The metatarsals of *D. leakeyi* are remarkable for their length. Mt.IV is longer than the Mc.IV of *Dicerorhinus* or *Aceratherium* from the same Rusinga deposits (M.18814). In *D. primaevus* (Arambourg 1959 : 72 and 68) Mt.IV is longer than Mc.IV although Mt.III is shorter than Mc.III. In *D. sumatrensis* there is only a slight difference in length between Mt.IV and Mc.IV. In general, metatarsals are more shortened than the metacarpals within the same species.

The metatarsals of *D. schleiermacheri* are unknown ; its metacarpals, however, are longer than those in *orientalis*, *ringstroemi*, and *primaevus*, and probably would have exceeded those of *D. leakeyi* in length. An Mt.III of *D. orientalis* from Pikermi recorded by Gaudry (1862–67 : 207, pl. 32, fig. 9) has a length only of 160 mm. by a greatest distal width of 52 mm., less than in *D. leakeyi*. The metatarsals of *D. primaevus* are also shorter than those of *D. leakeyi*. Mt.II and Mt.IV of *D. primaevus* are relatively less expanded distally than in *D. sumatrensis*, as is also the case with Mt.II and Mt.IV of *D. leakeyi*. In all three forms the median metatarsal is approximately 10% longer than the metatarsals on either side of it, as it is in *Aceratherium incisivum* recorded by Ringström (1924 : 192) and listed in the last column of Table 49. In a set of metatarsals from Budenheim recorded as *A. incisivum* by Kaup (1834 : 61, pl. 15, fig. 9) the lengths are less than those studied by Ringström.

TABLE 49

Measurements of metatarsals of *Dicerorhinus* and *Aceratherium* (mm.)

	D. leakeyi	*D. primaevus*	*D. sumatrensis*	*Aceratherium ?* sp. Losodok	Viehhausen	Freimann	Budenheim	(Ringström)
Mt. II, median length	162	149	126	—	140	—	135	146
Proximal width	29	—	29	—	21	—	—	—
Prox. ant. post. diameter	48	—	34	—	36	—	—	—
Middle width	32	—	30	—	23	—	—	30
Middle ant. post. diameter	30	—	21	—	20	—	—	—
Greatest distal width	42	35	40	—	—	—	—	—
Width of distal trochlea	36	—	35	—	26·5	—	—	—
Distal ant. post. diameter	41	—	39	—	33	—	—	—
Ratio middle width/length	0·20	—	0·24	—	0·16	—	—	0·21
Mt. III, median length	180	165	144	168	—	—	150	158
Proximal width	57	—	53	—	—	—	—	—
Prox. ant. post. diameter	49	—	37	—	—	—	—	—
Middle width	50	—	41	42	—	—	—	35
Middle ant. post. diameter	25	—	19	—	—	—	—	—
Greatest distal width	*c.* 60	52	53	46	—	—	—	—
Width of distal trochlea	51	—	44	—	—	—	—	—
Distal ant. post. diameter	41	—	38	—	—	—	—	—
Ratio middle width/length	0·28	—	0·28	0·25	—	—	—	0·22
Mt. IV, median length	160	147	126	160	140	126	140	145
Proximal width	44	—	41	—	33	40	—	—
Prox. ant. post. diameter	46	—	41	—	36	36+	—	—
Middle width	29	—	25	33	21	28	—	—
Middle ant. post. diameter	—	—	21	—	25	23	—	—
Greatest distal width	38	38	37	39	—	—	—	—
Width of distal trochlea	37	—	32	—	25	30	—	—
Distal ant. post. diameter	40	—	38	—	32	33	—	—
Ratio middle width/length	0·18	—	0·20	0·21	0·15	0·22	—	—

The Mt. III and Mt. IV from Losodok described by Arambourg (1933 : 11, pl. 1, figs. 4, 5) were noted to be nearly identical in dimensions with those of *Aceratherium tetradactylum*, but differing in their wider extremities and the shape of their articular surfaces. The fourth metatarsal Arambourg noted to be longer and more slender than that in the Sansan *Aceratherium* (*tetradactylum*). Arambourg (1933) preferred to leave the generic identity of the Losodok bones uncertain, naming them "*Aceratherium*? sp.". The Mt. IV of *D. leakeyi*, it will be observed, corresponds with its homologue from Losodok in length and distal width, but has a more slender shaft.

The Rusinga Mt.IV is intermediate in relative shaft width between a slender Mt.IV of *Aceratherium tetradactylum* from Viehhausen (Rinnert 1956 : 34) and one from Freimann recorded by Stromer (1928 : 29) as probably referable to *A. tetradactylum.* In the Aquitanian of Laugnac there is a very slender Mt.IV figured by Repelin (1917 : 40, pl. 6, figs. 3, 4) as " un type spécial de Rhinocérotidé " that has a great resemblance to the same bone in *A. tetradactylum* (which is Vindobonian) ; its length is 130 mm., and its middle width only 20 mm., giving a ratio of 0·15. The Laugnac bone is found in the same deposits as *Aceratherium lemanense* (= *Teleoceras aginense* Repelin : Lavocat 1951 : 114) that has less slender metapodials (Mt.IV length 99–103 mm., middle width 28–30 mm.). The Mt.III from Losodok nearly falls within the range of length of this bone in *A. tetradactylum* as given by Osborn (1900 : 246 : Mt.III 135–165 mm.) ; the Rusinga Mt.III is longer but relatively less slender. The Rusinga Mt.II is again less slender than that from Viehhausen recorded by Rinnert (1956 : 34, pl. 3, fig. 4), but is about equal in relative shaft width to that of *A. incisivum* as given by Ringström. A right Mt.II from the Upper Burdigalian of La Romieu figured by Roman & Viret (1934 : 36, pl. 9, fig. 12) is about 128 mm. in median length and very slender (no measurement given), just as is that from Viehhausen. The La Romieu bone has been identified only as " *Ceratorhinus* sp.? ".

The conclusions from all this may only be that we are not able as yet to distinguish between the metapodials of *Dicerorhinus* and *Aceratherium.*

Two proximal portions of right second metacarpals have to be recorded, viz., M.18844, R.1, Rusinga (proximal width 32 mm., ant. post. 46 mm.), and M.18847, Rs.105, Rusinga (proximal width 29 mm., ant. post. 49 mm.). These bones are very much like their homologue in the skeleton of *D. leakeyi.*

All of the phalanges of the left hind foot of the skeleton of *Dicerorhinus leakeyi* no. 2, R.1, 1947, are present (Pl. 13, fig. 3), and only the third phalanx of the median digit is incomplete. Of the right hind foot there are the first and second phalanges of the median digit (Pl. 10, figs. 4, 5), and none of the other digits. Measurements will be found in Table 50.

TABLE 50

Measurements of posterior phalanges of *Dicerorhinus* (mm.)

	D. leakeyi			*D. primaevus* lateral digit	*D. sumatrensis*		
	I	III	IV		II	III	IV
Phalanx I, length	37	40	33	42	31	35	30
Proximal width	40	55	38	48	38	47	35
Phalanx II, length	27	31	25	37	23	27	22
Proximal width	37	58	35	33	33	48	32
Phalanx III, length	33	—	30				
Greatest diameter	60	—	58				

In *D. leakeyi* as well as in *D. sumatrensis* the phalanges of digit IV are smaller than those of digit II. The width of the second phalanx of the lateral digit of *D. primaevus*

(Arambourg 1959 : 69) is probably 43 instead of 33 mm. Comparison with Table 37, in which the measurements of the anterior phalanges are given, shows that the lateral digit phalanges are more reduced in size relative to those of the median digit in the hind foot than in the fore foot.

To end the account of the foot skeleton of *Dicerorhinus leakeyi* mention should be made of the sesamoids. Some of the proximal sesamoid bones of the left hind foot are preserved *in situ*. The two situated behind the distal end of metatarsal III are 41 mm. long and 22 mm. wide ; those attached to metatarsal II are 32 mm. long by a width of 17 mm. In *D. sumatrensis* the proximal sesamoids have the same width (17 mm.) ; those of the median digit are 38 mm. long, and those of the second digit 30 mm.

There remains a number of distal ends of metapodials, phalanges, and sesamoid bones enumerated here for the sake of completeness. The specimens definitely belonging to *Brachypotherium* have been sorted, and are recorded under *B. heinzelini*. Those listed in the following pages are either *Dicerorhinus* or *Aceratherium*.

Distal ends of median metapodials (measurements in mm.)

	Greatest width	Trochlea width	Ant. post. diameter
No. 430, Karungu, 1947	57	45	—
M.18818, Rusinga	—	45	38
M.18823, Rs.101, Rusinga	—	51	—
M.18836, Ombo	*c.* 53	*c.* 44	41
M.18834, marked N_1	58	48	42

Distal ends of lateral metapodiais

M.18829, R.1, Rusinga	38	34	—
M.18825, Rusinga	38	35	32
M.18826, Rs.31, Rusinga	39	37	34
M.18821, Rusinga	—	34	31
M.18824, Rusinga	39	34	34
M.18820, Rusinga	—	—	39
M.18832, R.1, Rusinga	—	41	39
M.18819, Rs.81, Rusinga	—	35	—
M.18833, R.1, Rusinga	43	40	39
M.18816, Rs.31, Rusinga	38	35	36
M.18817, Rs.31, Rusinga	—	*c.* 39	—
M.18831, Rusinga	—	32	33
M.18827, Rs.105, Rusinga	42	38	40
M.18815, R.2, Rusinga	—	39	43
M.18828, Rs.3, Rusinga	40	35	35
M.18835, Kachuku, Lower Series, Karungu	—	33	—
M.18830, Rusinga	—	34	32

Phalanx I, median digit (measurements in mm.)

	Length	Prox. width
M.18858, R.1, Rusinga	38	55
No. 938, 1947, Gumba red-beds, Rusinga	34	55
No. 197, 1947, S. of Kiahera Hill, Rusinga	33	52
No. 237, 1950, R.2–4, Rusinga	37	48
M.18860, Rs.31, Rusinga	34	48

Phalanx II, median digit

M.18863, Rs.30, Rusinga	27	48
M.18861, Rusinga	29	43
M.18864, Rs.30, Rusinga	24	53
M.18867, Ngira, Karungu	25	42
No. 1060, S.E. of Kiahera Hill, Rusinga	22	—

Phalanx I, lateral digit

	Length	Prox. width
M.18856, Rusinga	36	38
M.18857, Rusinga	35	38
No.1152, R.2–4, Rusinga, 1950	29	35
M.18853, Rs.31, Rusinga	28	40
M.18868, Ngira, Karungu	31	39

Phalanx II, lateral digit

M.18855, Rs. 104, Rusinga	24	36
M.18866, Rs.30, Rusinga	22	37
M.18865, Rusinga	21	27
No. 110, 1949, W. Hiwegi, Rusinga	22	29

There remain one third phalanx of a median digit, no. 498, Rusinga, 1950 (length 24 mm., greatest width 63 mm.), a third phalanx of a lateral digit, M.18852, Rusinga (length 40 mm., greatest diameter 64 mm.), and an incomplete third phalanx of a lateral digit, no. 845, Kathwanga, Rusinga (length 29 mm.).

Proximal sesamoids, median digit

	Length	Width
M.18871, Rusinga	48	25
No. 921, 1947, N. of Kiahera Hill, Rusinga	49	26
M.18869, Rs.6a, Rusinga	47	25
M.18874, Rs.21, Rusinga	45	24
No. 238, 1950, R.2–4, Rusinga	43	26
M.18870, R.1, Rusinga	40	21
No. 536, Chianda Uyoma	40	24
M.18873, Rs.21, Rusinga	—	23
No. ? (possibly belonging to skeleton no. 2, R.1, 1947)	40	21

Proximal sesamoids, lateral digit

No. 239, 1950, R.2–4, Rusinga	34	16
M.18872, Rs.38, Rusinga	32	17
No. 820, 1947 (possibly belonging to skeleton no. 2, R.1, 1947)	31	20
No. 820, 1947 (idem, second specimen)	30	18
No. ? (idem)	30	17
No. ? (idem)	31	16

What is probably the distal sesamoid (situated behind the junction of the second and third phalanges) of the median digit (unnumbered, possibly belonging to skeleton no. 2, R.1, 1947) is 31 mm. wide transversely and 7 mm. high at the articular surface.

The tail vertebrae labelled as belonging to the skeleton no. 2, R.1, 1947, of *Dicerorhinus leakeyi* range from what is probably the fourth from the sacrum to nearly the last. The largest vertebra has only the left transverse process, 42 mm. in anteroposterior diameter (23 mm. in *D. sumatrensis*), and an arch that appears to have been higher than the body but crushed dorso-ventrally. The spinous process has a thickened summit. The greatest width of the vertebra is about 95 mm. (73 mm.). The second largest caudal vertebra has both transverse processes, greatest width 82 mm. (69 mm.), but these processes are much reduced anteroposteriorly to 21 mm. (14 mm.). The small and distorted arch is bifid behind, and probably not higher than the body.

An isolated double summit of an arch intermediate in size between the last and the vertebrae to be mentioned next indicates that the body of at least one caudal vertebra has been lost. The next has a body still as long as that of the second largest of the lot, viz., 39 mm. (29 mm.), only traces of a transverse process, and a very small arch, which was probably open dorsally. This vertebra is crushed laterally.

Of the remaining thirteen caudal vertebrae only the largest two have two ridges dorsally, the others being without a trace of an arch. These vertebrae are not distorted and seem to form an unbroken series. The length and anterior height of the body decrease from 35 and 27 mm. in the first, over 26 and 12 mm. in the middle (seventh) of the series, to 16 and 8 mm. in the last. The caudal vertebra in *D. sumatrensis* that shows the same reduction of the arch as the anterior of our series of thirteen is the ninth caudal; it is 25 mm. long and 23 mm. high anteriorly. The fifteenth caudal vertebra in *D. sumatrensis* is 26 mm. long and 14 mm. high, while the twenty-first is 19 mm. long and 7 mm. high. It is followed by three more vertebrae, the last one of which has a pointed end.

From this comparison it follows that the tail vertebrae of *D. leakeyi* reduce in length more rapidly as one passes along the series than in the corresponding section of the tail of *D. sumatrensis*, that the relative anterior height is greater half-way along the tail in *D. sumatrensis*, but that it diminishes more rapidly toward the end than in *D. leakeyi*.

III. DISTRIBUTION OF RHINOCEROSES OVER EAST AFRICAN MIOCENE SITES

In Table 51 are given the locality records of those specimens of which the generic position has been determined.

TABLE 51

Distribution of Rhinocerotidae in the East African Miocene

	Dicerorhinus	*Aceratherium*	*Brachypotherium*	*Chilotherium*
Rusinga (no sub-site given)	×	×	×	.
R.1	×	×	×	.
R.1–1a	×	.	×	.
R.2	×	.	.	.
R.2–4	×	×	.	.
Rs.3	×	.	.	.
Rs.6a	.	.	×	.
R.7, Rs.7	.	.	×	.
R.11	×	.	.	.
Rs.26	×	.	.	.
R.73	.	.	×	.
Rs.91	.	×	.	.
Rs.101	.	.	×	.
R.107	.	×	.	.
Rs.108	×	.	.	.
Gumba	×	×	×	×
West side of Hiwegi	×	.	×	.
Kamasengere	.	×	.	.
Kathwanga	×	.	×	.
S. of Kiahera Hill	.	×	.	.
S.E. of Kiahera Hill	.	.	×	.
Wakondu	.	.	.	×
Karungu (Andrews 1914 and 1937)	.	.	×	.
Ngira, Karungu	.	×	×	.
Songhor	×	.	.	.
Moruaret Hill (Deraniyagala)	.	×	.	.
Loperot	.	.	.	×
Napak I	.	×	.	.
II A and C	.	.	×	.
V	×	.	.	.
VI	×	.	.	.

Generically uncertain material of Rhinocerotidae has also been obtained from subsites of Rusinga and other sites in Kenya whence no generically identifiable rhinoceros specimens have come, as follows :

R.4 (astragalus), R.8 (cuboid), Rs.21 (radius, astragalus, two proximal sesamoids), Rs.23a (scapula), Rs.30 (ectocuneiform, two phalanges II of median digits, phalanx II of lateral digit), Rs.31 (radius, unciform, Mc.III–IV, patella, tibia, astragalus, three lateral metapodials, phalanx I of median digit, phalanx II of lateral digit), Rs.38 (astragalus, proximal sesamoid), Rs.81 (lateral metapodial), Rs.103 (Mc.III), Rs.104 (phalanx II of lateral digit), Rs.105 (Mc.II, tibia, cuboid, ectocuneiform, lateral metapodial), R.106 (astragalus, calcaneum), Kiahera Hill (P_2), N. of Kiahera Hill (proximal sesamoid), Kiangata (lower C), Kiune (astragalus), and the following sites other than Rusinga: Aloir, 1939 (mandibular ramus and astragalus), Chianda Uyoma (proximal sesamoid), Ombo (median metapodial), Maboko (= Kiboko) Island (two scaphoids, tibia, astragalus), Kachuku, Lower Series, Karungu (Mc.II–III, cuboid, lateral metapodial), Kachuku, Karungu (cuboid), Losodok (Arambourg, 1933) (lower M, axis, astragalus, Mt.III–IV, three phalanges I of median and lateral digits), and Arongo Chianda, 25.x.1939 (astragalus).

I have not seen any material from Tambach, and am unable to confirm the record of rhinoceros from that locality (cf. Le Gros Clark & Leakey 1951 : 5). In addition to the nine sites in Kenya from which Rhinocerotidae have been recorded in 1951 there are Aloir, 1939, and Arongo Chianda, 25.x.1939, both with a generically unidentifiable non-brachypothere astragalus. All groups of mammals found in Rusinga are known to be represented at Mfwanganu Island, Kenya, except for the rhinoceroses and insectivores (Whitworth 1961), and indeed the only rhinoceros-like specimen that I have seen from that island, a proximal metapodial fragment, is *Brachyodus aequatorialis* MacInnes, the large Rusinga anthracothere, which will be reported later.

IV. TIME PLACEMENT OF THE MIOCENE EAST AFRICAN FAUNAS

The Miocene faunas of East Africa are generally regarded as Early Miocene, corresponding to the Burdigalian stage of Europe. Dr. Leakey kindly informs me that the geology of Rusinga is much more complicated than had been previously thought, and not all of it may be of the same age. Loperot, at present being investigated by the Harvard Expedition, is a considerable area with many different sites that may not be contemporaneous. Most of the Loperot sites are probably much younger than most of Rusinga. Further studies on elements of the *Proconsul* fauna are being undertaken. Potassium-Argon dates have been published during the last few years, and are still being worked on, and these have not invariably had the mammalian palaeontologists' approval.

From a number of K/A dates for Rusinga, including two of over 100 million years (!), Evernden, Savage, Curtis & James (1964 : 176 : KA 336) consider 15·3 ± 1·5 million years the best estimate and only meaningful age; this would approximately correspond with Late Miocene (Vindobonian). However, the age that has recently been determined for Napak, Uganda, viz., 19 ± 2 million years (Bishop 1964) points to Early Miocene (Burdigalian). A Middle Miocene age for Rusinga has been proposed on faunal grounds by Thenius (1959 : 268), and the geological setting of the Western Rift deposits of Congo, whence a typical Rusinga fauna has been described (Hooijer 1963), even leaves room for a Late Miocene age of part of the fauna. The slightly different faunules of Malembe and Bololo in the Atlantic coastal region of Congo are Burdigalian as the associated fish fauna indicates (Hooijer 1963 : 5, 64). Radiometric dates are not as yet available for the various Western and Eastern Congo sites.

What now is the bearing of the Rhinocerotidae of Rusinga and Napak on the problem of the age of these deposits? Let us summarize the salient characters and similarities to European Tertiary rhinoceroses.

Of the four genera and species of Rhinocerotidae from Rusinga and other Miocene sites in East Africa two are in keeping with either Burdigalian or Vindobonian, and two rather with Vindobonian, in the European sense. *Aceratherium acutirostratum* is unique in the combination of a shallow naso-maxillary notch (Aquitanian in Europe) and an elevated occiput (Pontian in Europe). Its teeth are more advanced in structure than those in the European Oligocene forms ; either Burdigalian or Vindobonian would seem fitting for this species. *Chilotherium*, now found for the first time in Africa (the two Rusinga M need not be specifically the same as the Loperot M^3)[1], ranging from Burdigalian into the Pontian in Asia and from Vindobonian into Pontian in Europe, could be either Burdigalian or Vindobonian as well ; the earliest chilotheres are as fully-fledged as the Pontian (Cooper 1934 : 596). *Dicerorhinus leakeyi* has the skull shape of the Vindobonian *D. sansaniensis* although it is larger, and its teeth agree in characters with those of this as well as some larger Pontian forms. It has no close relationship with tapir-sized, slender-footed Aquitanian and Burdigalian *D. tagicus*. *Brachypotherium heinzelini* almost duplicates the Late Vindobonian *B. brachypus* ; only its lateral metacarpals are relatively shorter and wider. It is definitely more advanced in progressive metapodial abbreviation than the Moghara *B. snowi*, which has only reached the stage of the Late Burdigalian and Early Vindobonian *B. stehlini*. The four forms occur together in the Gumba beds of Rusinga.

The same assemblage of rhinoceroses, except for the rarest *Chilotherium* sp., occurs at Napak, K/A dated as Early Miocene, Burdigalian. The fauna of Napak is exceedingly similar to that of the Kenya sites ; in the latest survey of the fauna (Bishop 1962) this was brought out by various specialists. Rhinocerotidae and Anthracotheriidae were not mentioned in the 1962 paper as no data were available at the time. Among the dental material from Napak kindly sent to me from time to time by Dr. W. W. Bishop there is a very characteristic upper molar of *Brachyodus aequatorialis* MacInnes (1951), indistinguishable from the Rusinga type. The specimen originates from Napak II C, and other from Napak V and VIII, and from Moroto I and II ; this will be described later. Thus, the faunal likeness between Napak and Rusinga is further enhanced by the Anthracotheriidae as well as by the Rhinocerotidae.

The fauna of Fort Ternan, a site already famous for *Kenyapithecus wickeri* Leakey (1962), more advanced than *Proconsul*, has a totally different aspect. It comprises a small *Trilophodon* and a suid more evolved than the Rusinga forms, ruminants with incipient horns (unknown in the Miocene), and a highly intriguing form transitional between *Brachyodus* and hippo (Leakey, *in* Howell & Bourlière (editors), 1963 : 554). Anthracotheres are considered ancestral to hippopotami ; for these animals no other ancestry can be made plausible. *Brachyodus* occurs in the Burdigalian of Europe, and the first *Hippopotamus* appears in the Pontian of Europe (Hooijer 1946*c* ; Aguirre 1963). The Fort Ternan anthracothere or ancestral hippopotamus, therefore, would best be accorded a Vindobonian or very early Pontian age. Now this is just what the radiometric datings indicate : ± 12 million years (Leakey, *in* Howell & Bourlière

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[1] The results of the extensive Harvard Expedition to Loperot, which include parts of four skeletons, will be reserved for a later paper.

1963 : 554), 14 million years (Leakey 1963 : 138 ; Evernden, Savage, Curtis & James 1964 : 174). We might therefore say that Fort Ternan has been K/A dated to the satisfaction of the mammalian palaeontologist. The rhinoceroses of Fort Ternan have not yet been described, but with this fauna are bound to be different from the Rusinga and Napak species ; their study is eagerly awaited.

The " best estimate " of a date for Rusinga, 15·3 ± 1·5 million years as propounded by Evernden *et al.*, would seem to differ too little from that of Fort Ternan (12–14 million years) for such a faunal change to have taken place. A date like that of Napak (19 ± 2 million years) seems much more fitting for Rusinga, and is in keeping with palaeontological data. A fauna cannot well remain virtually unchanged for a period of several million years (if the difference in K/A dates for Napak and Rusinga amounts to that much ; both have appreciable standard errors, and the difference may be more apparent than real). One might therefore well wonder whether Rusinga has not been considered too young.

The Rhinocerotidae of Rusinga and Napak, as we have seen, would broadly correspond with the Burdigalian and Vindobonian stages in Europe. Intercontinental correlation on forms of this kind is, however, only approximate. None of the East African species is identical with any in Europe ; they probably were products of independent evolution in Africa although contemporaneous in origin with those of Eurasia. The pre-Miocene history of the rhinoceroses in Africa is sadly unknown ; none are, for example, found in the Fayum Series, at which times there had been faunal interchange between Africa and Eurasia. In Africa, rhinoceroses appear first at the Rusinga stage (unless the so-called Burdigalian fauna of Moghara, Egypt, which shows little affinity to that of Rusinga, is older).

It is feasible that *Dicerorhinus leakeyi* and *Brachypotherium heinzelini* represent more progressive evolutionary stages than the forms living at the same time in Europe (and North Africa, witness the *Brachypotherium* of Moghara), and actually are as old as the Napak K/A date indicates. Exact correlations cannot be made on the fauna so far as known. We may say that the East African Miocene fauna is approximately equivalent to the Burdigalian of Europe, but application of this Depéretian term to the East African faunal stage may easily impart a false sense of precision.

At this stage, all that can be said is that most of the Rusinga sites are tentatively accepted as correlative with the Burdigalian, the Lower Miocene of Europe, but that some sites on the island and elsewhere in East Africa appear to be younger, later Miocene or even Pliocene.

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PLATE 1

Dicerorhinus leakeyi sp. nov., skull and associated mandible (holotype), Rusinga, 1935, right view. ×¼.

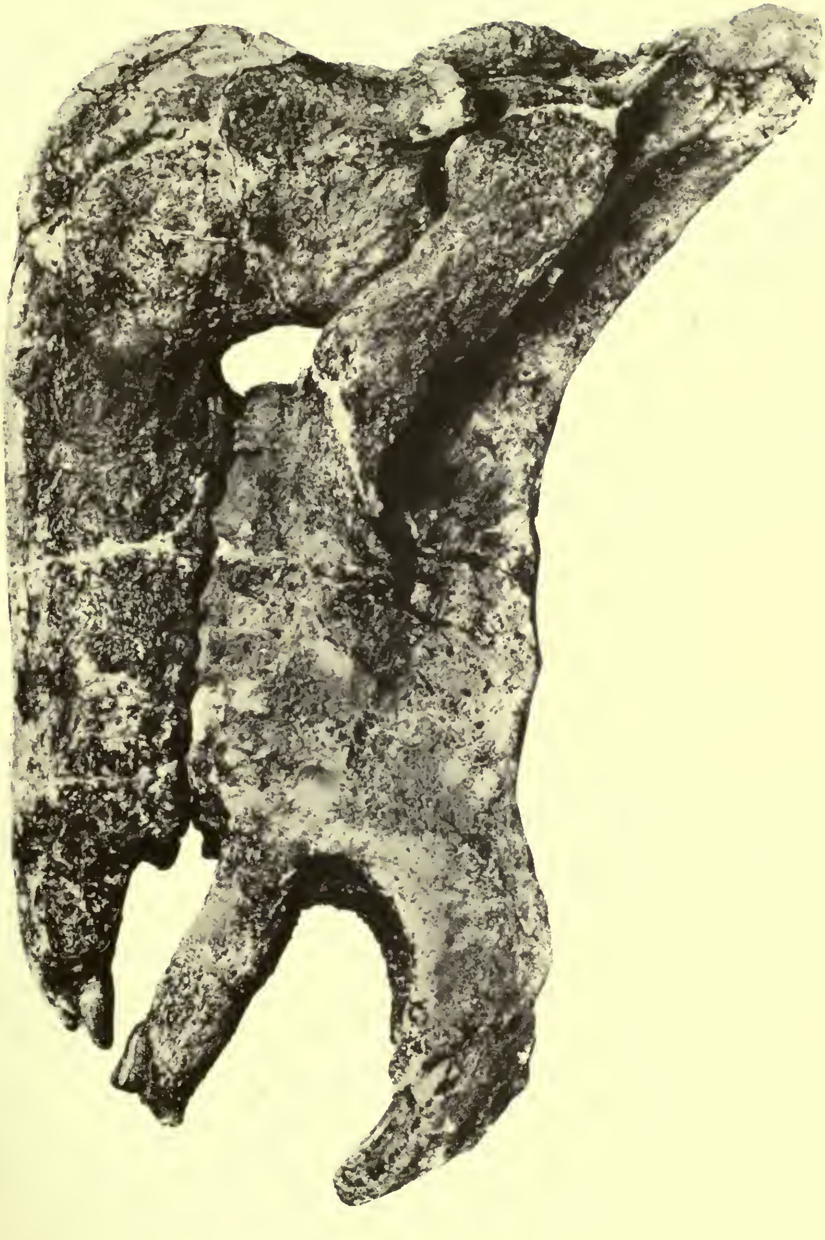
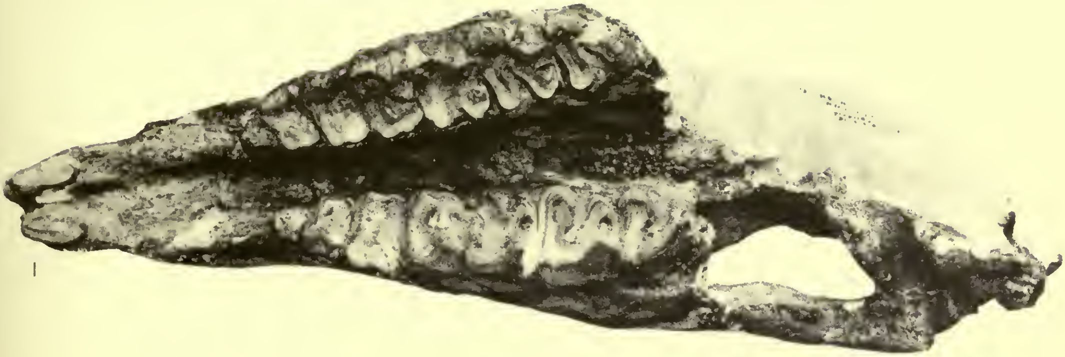


PLATE 2

Dicerorhinus leakeyi sp. nov.

FIG. 1. Holotype skull, Rusinga, 1935, lower view. ×¼.
FIG. 2. Holotype mandible, Rusinga, 1935, upper view. ×¼.
FIG. 3. P^2–M^3 dext., no. 2, R. 1, 1947, crown view. ×⅖.
FIG. 4. Mandible, no. 2, R. 1, 1947, right view. ×¼.



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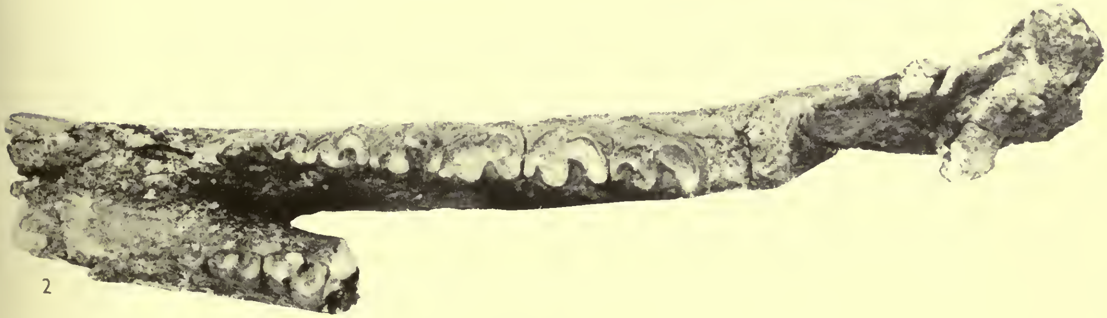

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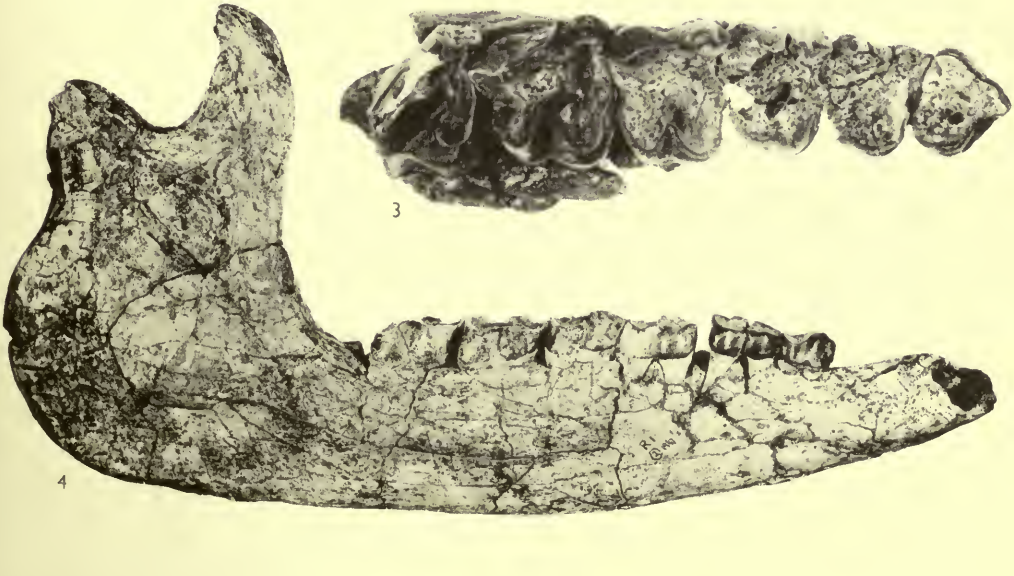

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PLATE 3

Excavation of skeletons of ***Dicerorhinus leakeyi*** sp. nov. and ***Aceratherium acutirostratum*** (Deraniyagala) at R.1, 1947. Dr. L. S. B. Leakey phot.

PLATE 3

PLATE 4

Dicerorhinus leakeyi sp. nov.

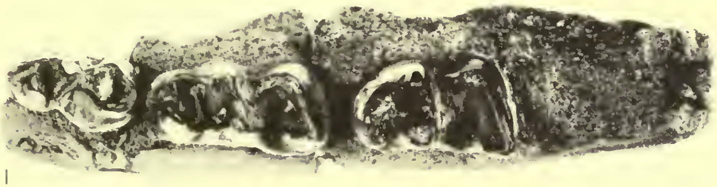
FIG. 1. DM_{2-4} dext., Napak V, 1962, crown view. $\times\frac{3}{4}$.
FIGS. 4, 5. Left and right lower C thought to belong to no. 2, R.1, 1947, upper view. $\times\frac{3}{5}$.
FIG. 7. Left upper I, no. 2, R.1, 1947, external view. $\times\frac{4}{5}$.
FIG. 8. Right upper I, no. 109, West side of Hiwegi, Rusinga, 1949, external view. $\times\frac{4}{5}$.

Aceratherium acutirostratum (Deraniyagala)

FIGS. 2, 3. Left and right lower C, no. 850, R.1, 1947, upper view. $\times\frac{3}{5}$.

Brachypotherium heinzelini Hooijer

FIG. 6. Right upper I, no. 79, R.1–1a, 1950, external view. $\times\frac{4}{5}$.



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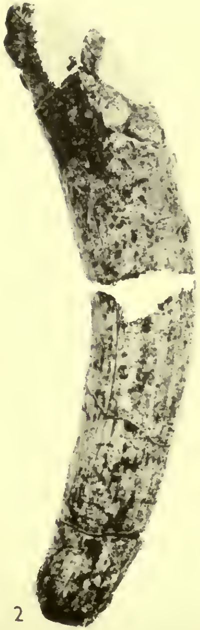

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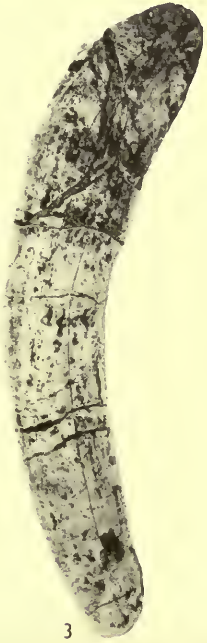

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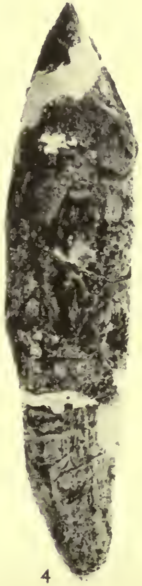

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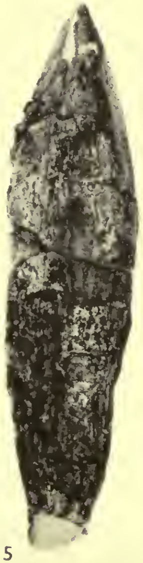

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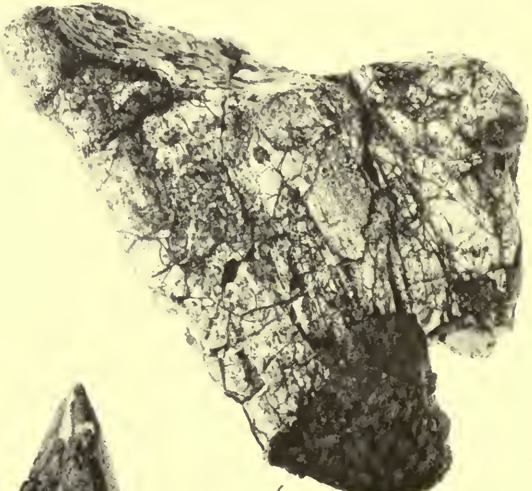

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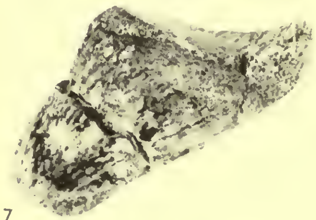

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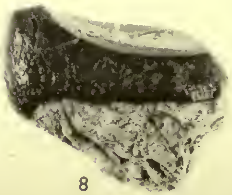

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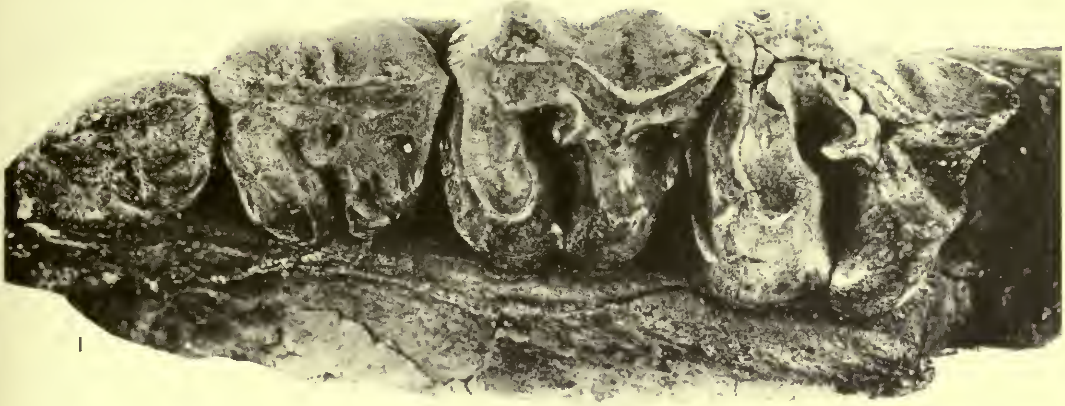
PLATE 5

Dicerorhinus leakeyi sp. nov.

FIG. 1. DM^{1-4} sin., Rs. 26, crown view. ×1.
FIG. 2. P^{3-4} sin., no. 2, R. 1, 1947, crown view. ×$\frac{4}{5}$.
FIG. 3. Same, internal view. ×$\frac{4}{5}$.

Aceratherium acutirostratum (Deraniyagala)

FIG. 4. DM^4 dext., no. 142, Kamasengere, Rusinga, 1949, crown view. ×$\frac{4}{5}$.
FIG. 5. DM^4 sin., no. 218, R. 107, 1948, crown view. ×$\frac{4}{5}$.



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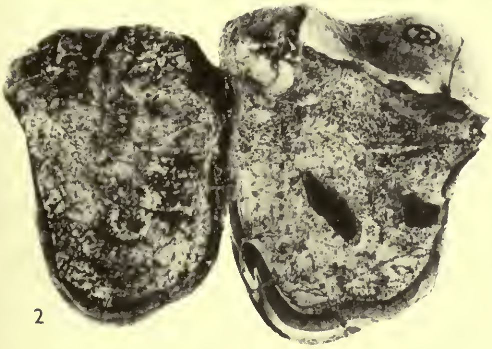

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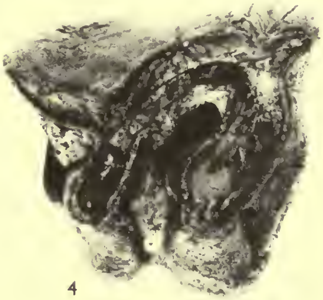

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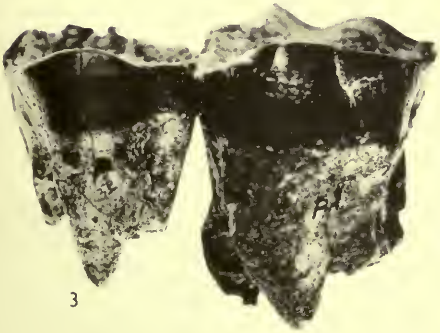

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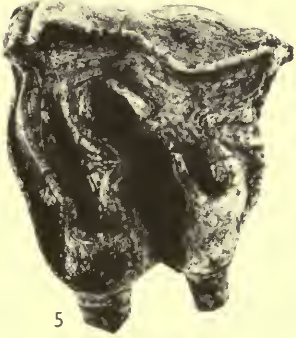

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PLATE 6

Aceratherium acutirostratum (Deraniyagala)

Fig. 1. P^4 sin., no. 232, R. 2–4, 1950, crown view. $\times \frac{4}{5}$.
Fig. 2. Same, internal view. $\times \frac{4}{5}$.
Fig. 3. P^4 dext. with portion of M^1, no. 231, R. 2–4, 1950, crown view. $\times \frac{4}{5}$.
Fig. 4. Same, internal view. $\times \frac{4}{5}$.

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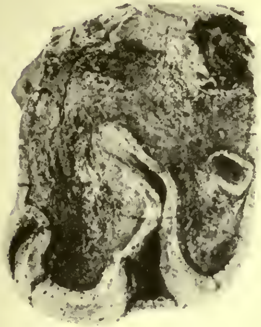
Fig. 5. M^1 dext., Karungu, 1937, crown view. $\times \frac{4}{5}$.
Fig. 6. Same, external view. $\times \frac{4}{5}$.
Fig. 9. Posterior portion of M_1 or M_2 sin., no. 546, R. 1, 1949, crown view. $\times \frac{4}{5}$.

Dicerorhinus leakeyi sp. nov.

Fig. 7. M^2 sin., no. 1161, R. 1, 1950, crown view. $\times \frac{4}{5}$.
Fig. 8. M_2 sin., no. 2, R. 1, 1947, crown view. $\times \frac{4}{5}$.
Fig. 12. P^3 dext., no. 1385, Rusinga, 1951. Crown view. $\times \frac{4}{5}$.

Chilotherium sp.

Fig. 10. M^1 or M^2 dext., no. 695, Gumba, Rusinga, 1949, crown view. $\times \frac{4}{5}$.
Fig. 11. Protoloph of right upper M, no. 506, Wakondu, Rusinga, 1950, crown view. $\times \frac{4}{5}$.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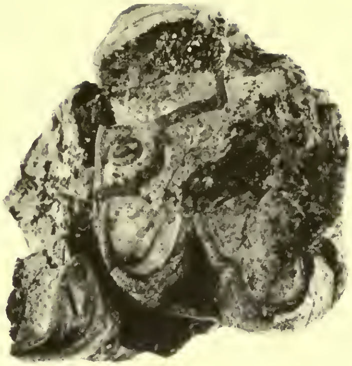
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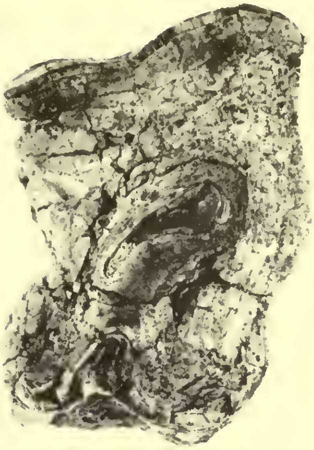
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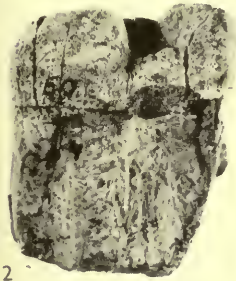
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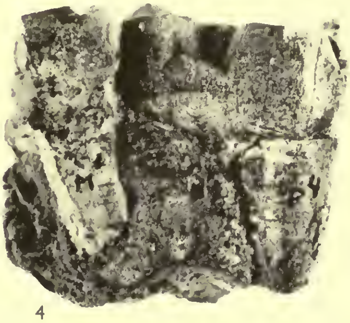
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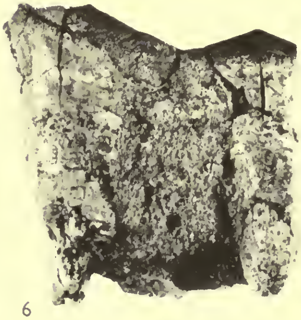
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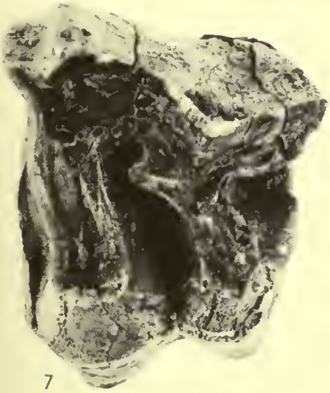
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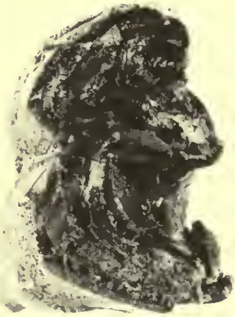
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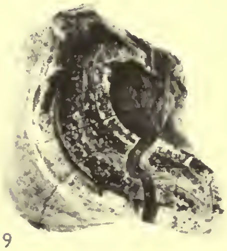
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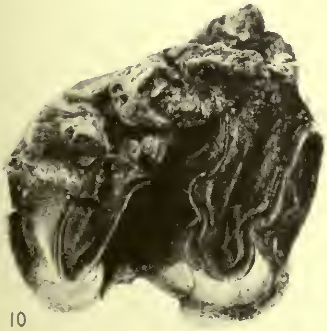
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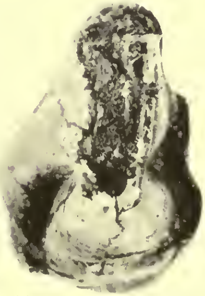
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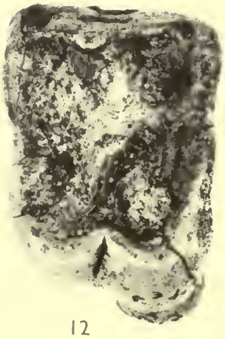
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PLATE 7

Chilotherium sp.

FIG. 1. M^3 dext., Loperot, 1948, crown view. $\times\frac{4}{5}$.
FIG. 2. Same, external view. $\times\frac{4}{5}$.

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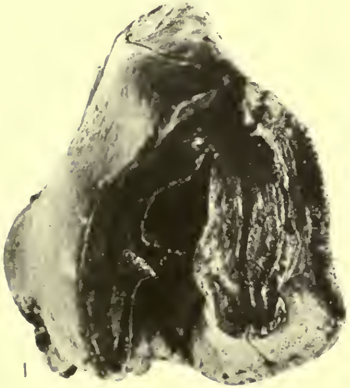
FIG. 3. M^3 dext., Karungu, 1913, M. 10632, crown view. $\times\frac{4}{5}$.
FIG. 4. Same, external view. $\times\frac{4}{5}$.

Dicerorhinus leakeyi sp. nov.

FIG. 5. M^3 sin., R. 1, crown view. $\times\frac{4}{5}$.
FIG. 6. Same, external view. $\times\frac{4}{5}$.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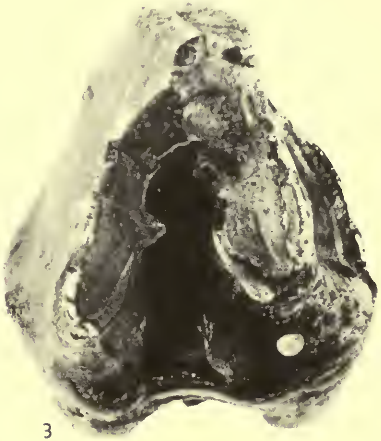
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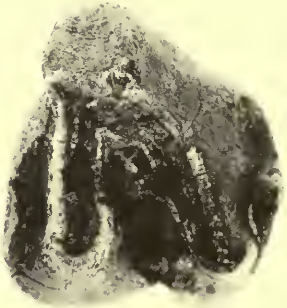
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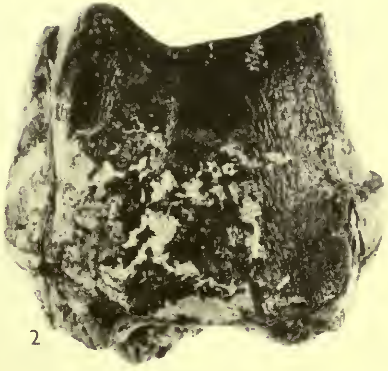
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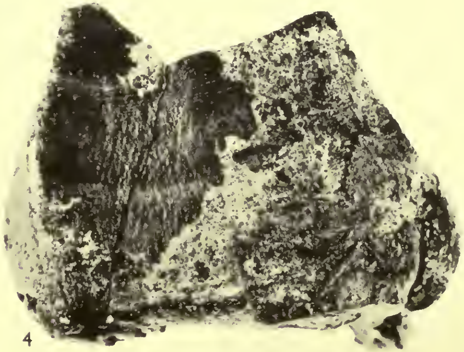
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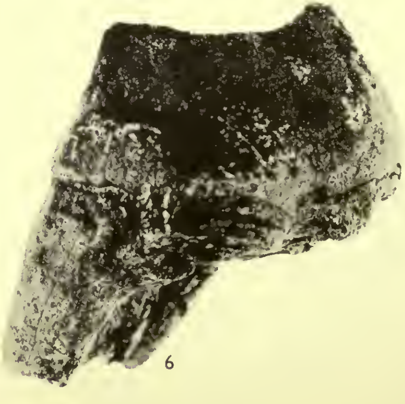
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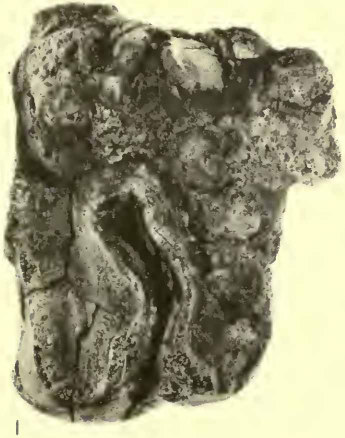
PLATE 8

Brachypotherium heinzelini Hooijer

FIG. 1. P^4 sin., Napak II C, 1964, crown view. ×$\frac{4}{5}$.
FIG. 2. M_2 sin., Napak IIA, 1964, crown view. ×$\frac{4}{5}$.
FIG. 3. P^{3-4} sin., no. 409, West side of Hiwegi, Rusinga, 1947, crown view. ×$\frac{4}{5}$.
FIG. 4. Same, external view. ×$\frac{4}{5}$.
FIG. 5. P^{3-4} dext., no. 270, R.73, 1949, crown view. ×$\frac{4}{5}$.
FIG. 6. Same, external view. ×$\frac{4}{5}$.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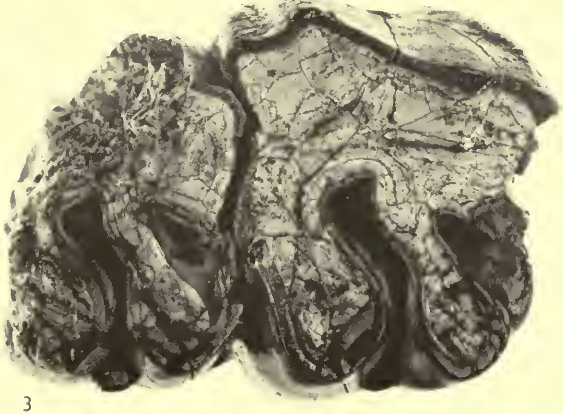
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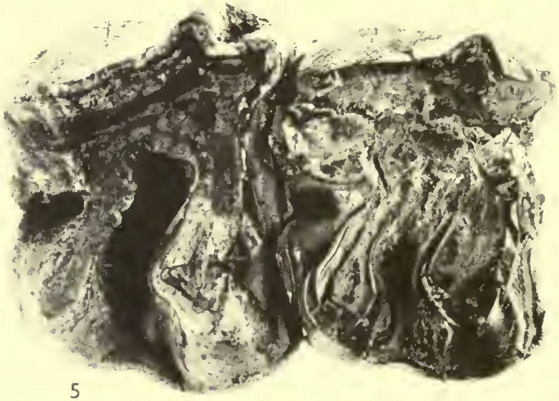
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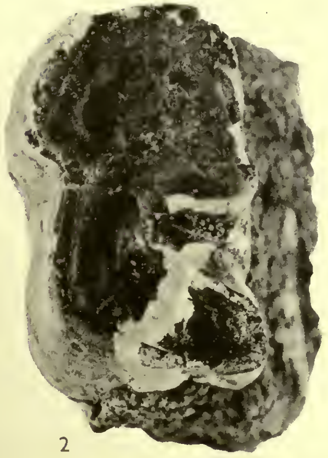
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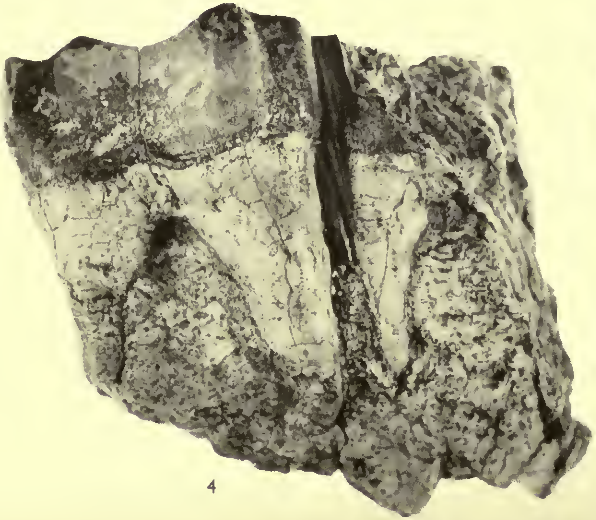
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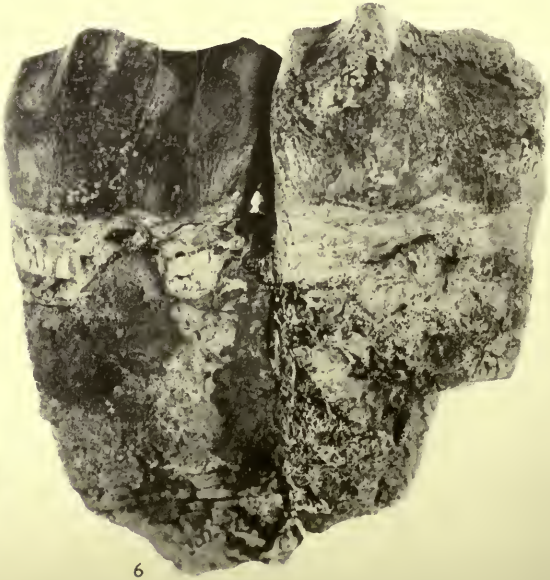
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PLATE 9

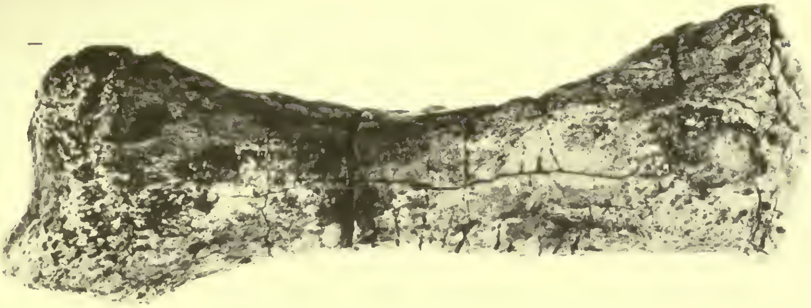
Brachypotherium heinzelini Hooijer

FIG. 1. Radius dext., M.18908, Rs.6a, anterior view. ×$\frac{1}{3}$.

Aceratherium acutirostratum (Deraniyagala)

FIG. 2. Radius sin., no. 850, R.1, 1947, anterior view. ×$\frac{1}{3}$.
FIG. 3. Nasals, no. 850, R.1, 1947, upper view. ×$\frac{2}{5}$.
FIG. 4. Mandible, no. 850, R.1, 1947, upper view. ×$\frac{2}{5}$.

1



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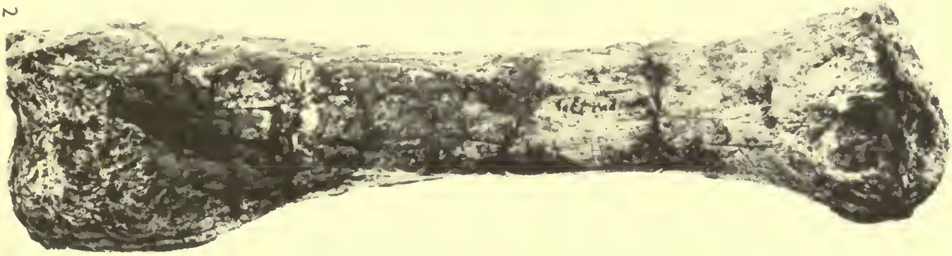

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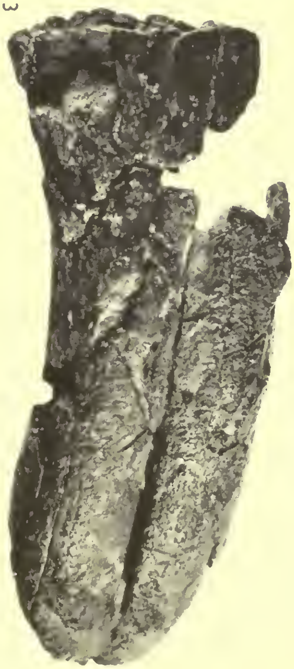

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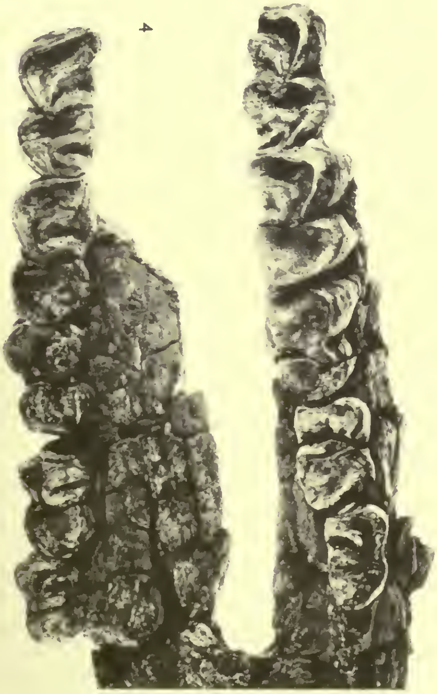


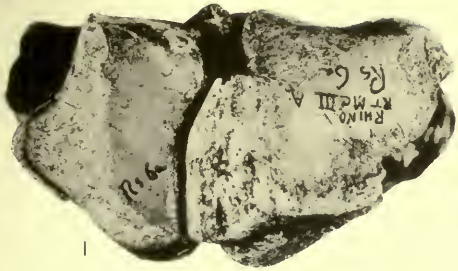
PLATE 10

Brachypotherium heinzelini Hooijer

FIG. 1. Mc.III–IV dext., M.18813 and M.18812, associated, Rs.6a, proximal view. ×⅗.
FIG. 2. Same, anterior view. ×⅗.
FIG. 3. Mc.II dext., F.3269, Rusinga, 1942, anterior view. ×⅗.
FIG. 6. Phalanx I of median digit, F.2126, Rusinga, 1941, anterior view. ×⅗.
FIG. 7. Phalanx II of median digit, M.18862, Rs.6a, anterior view. ×⅗.
FIG. 8. Mc.IV sin., M.18822, no. 451, Kathwanga, Rusinga, 1947, anterior view. ×⅗.

Dicerorhinus leakeyi sp. nov.

FIG. 4. Phalanx I of median digit of right pes, no. 2, R.1, 1947, anterior view. ×⅗.
FIG. 5. Phalanx II of median digit of right pes, no. 2, R.1, 1947, anterior view. ×⅗.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RT MC III A
R5 G

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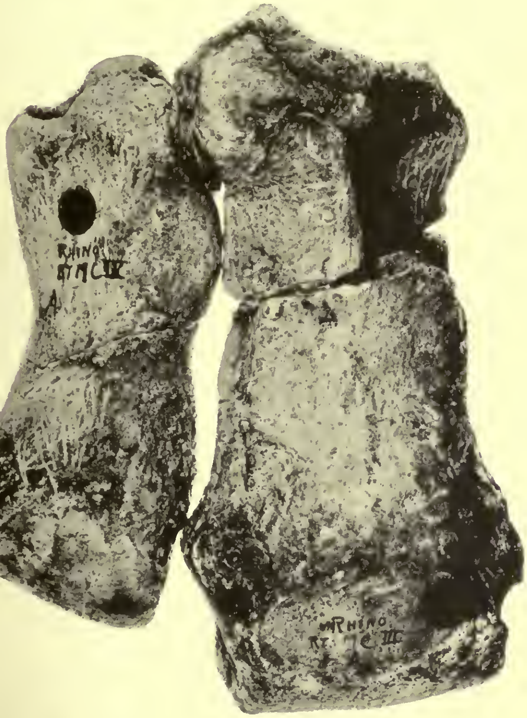
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A
RHINO
RT MC III

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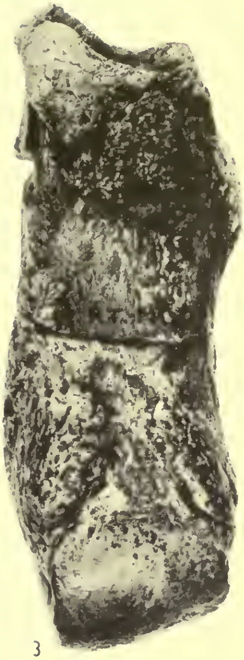

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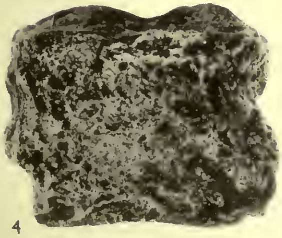

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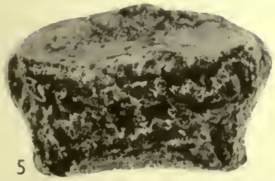

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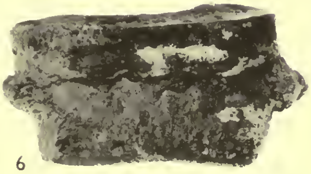

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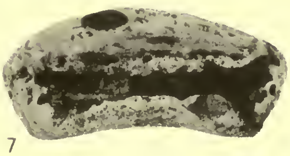

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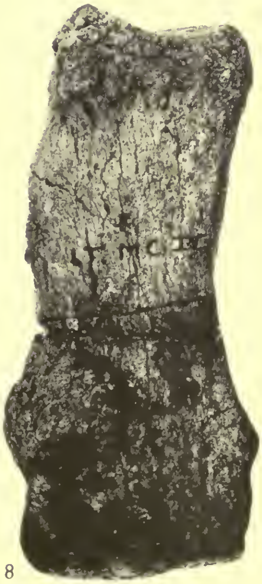


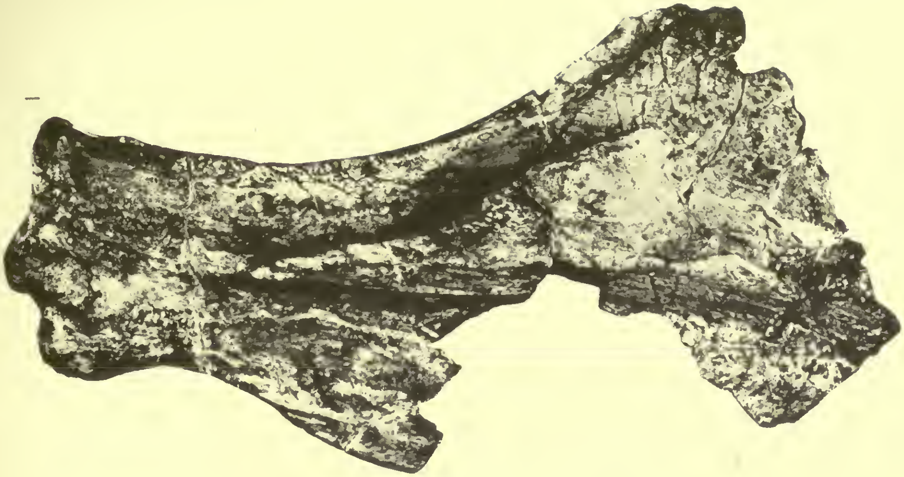
8

PLATE 11

Dicerorhinus leakeyi sp. nov.

FIG. 1. Scapula dext., no. 2, R.1, 1947, lateral view. ×$\frac{1}{4}$.
FIG. 2. Humerus dext., no. 2, R.1, 1947, posterior view. ×$\frac{1}{4}$.
FIG. 3. Radio-ulna sin., no. 2, R.1, 1947, lateral view. ×$\frac{1}{4}$.

1



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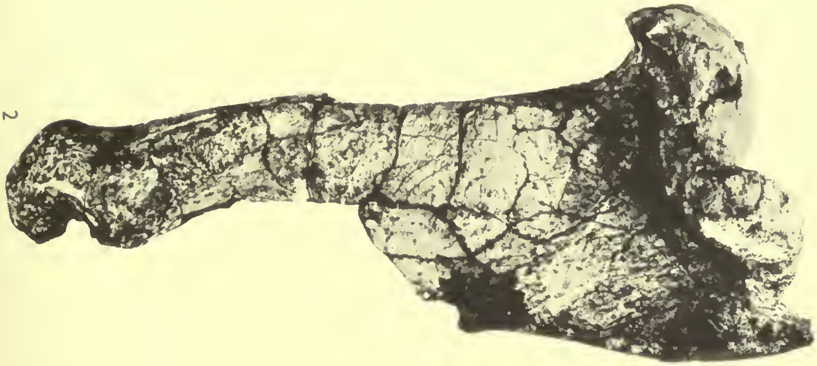

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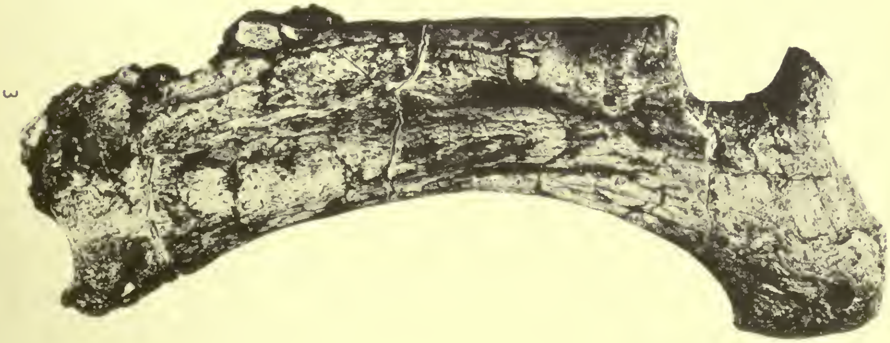
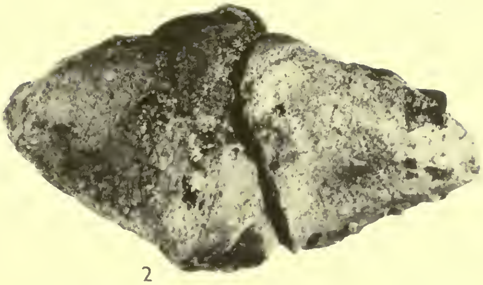


PLATE 12

Dicerorhinus or ***Aceratherium*** sp.

FIG. 1. Mc.IV dext., M.18811, Rusinga, anterior view. × $\frac{3}{5}$.
FIG. 2. Mc.III–IV sin., M.18841 and M.18814, associated, R.1, proximal view. × $\frac{3}{5}$.
FIG. 3. Same, anterior view. × $\frac{3}{5}$.
FIG. 4. Mc.II–IV sin., M.18842 (Rs.), M.18837 and M.18840 (Rs.31), anterior view. × $\frac{3}{5}$.



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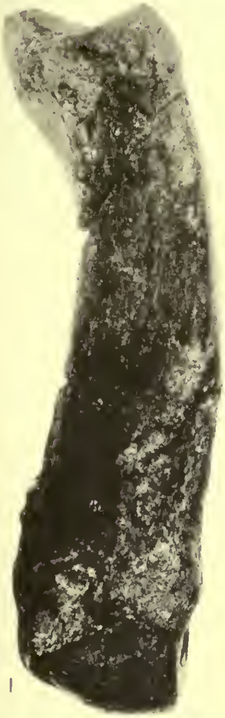

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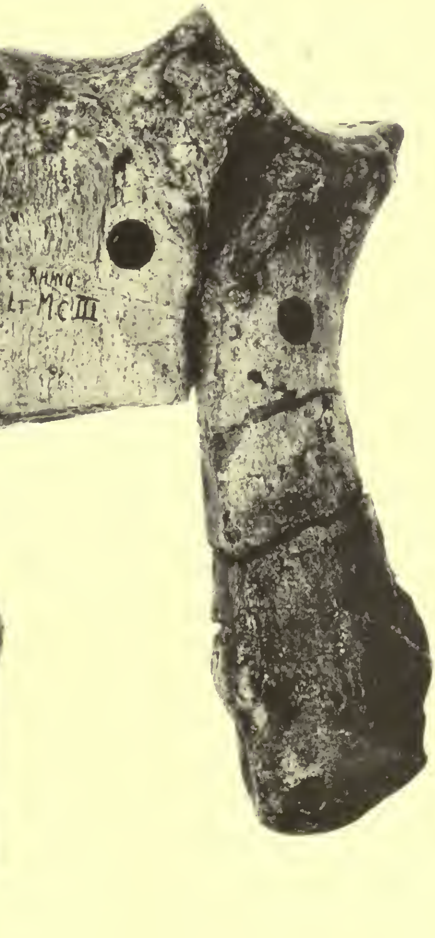
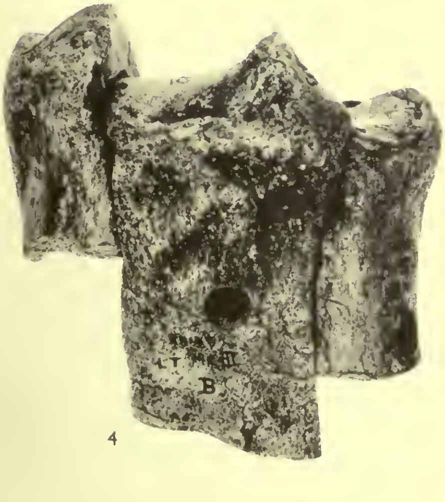

RHINO
LT MC III

3



4

PLATE 13

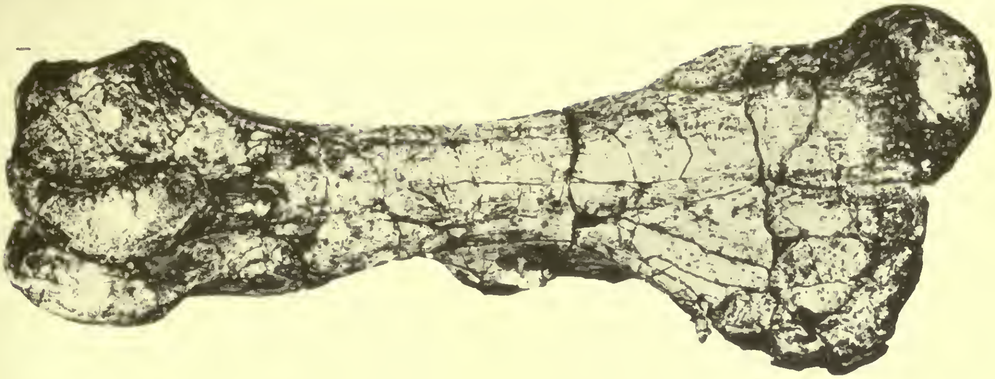
Dicerorhinus leakeyi sp. nov.

FIG. 1. Femur sin., no. 2, R.1, 1947, anterior view. $\times\frac{1}{4}$.
FIG. 2. Tibio-fibula sin., no. 2, R.1, 1947, anterior view. $\times\frac{1}{4}$.
FIG. 3. Pes sin., no. 2, R.1, 1947, anterior view. $\times\frac{1}{4}$.
FIG. 4. Cuboid sin., no. 2, R.1, 1947, lateral view. $\times\frac{2}{3}$.
FIG. 5. Same, anterior view. $\times\frac{2}{3}$.

Dicerorhinus or ***Aceratherium*** sp.

FIG. 6. Cuboid dext., M.18890, R.1, anterior view. $\times\frac{2}{3}$.

1



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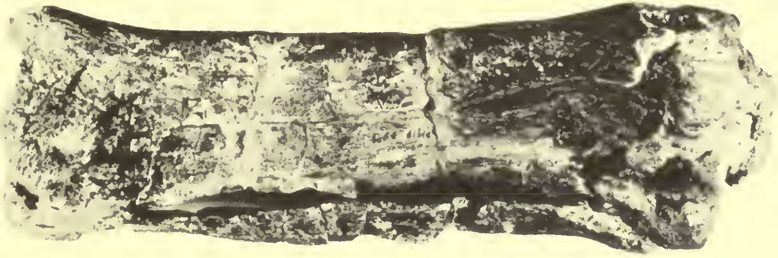

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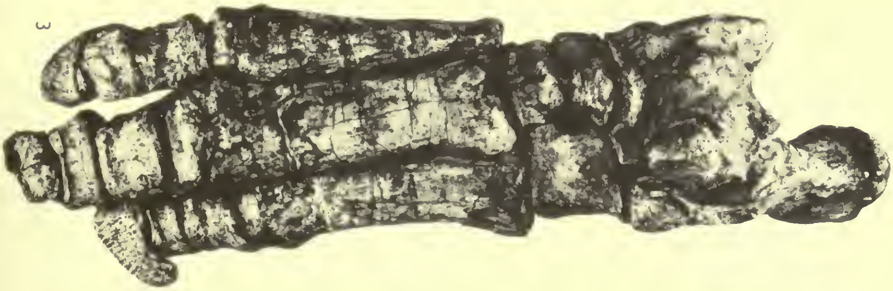

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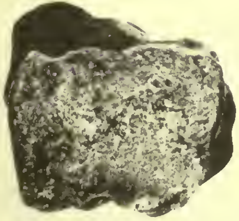

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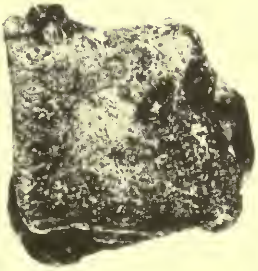

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PLATE 14

Dicerorhinus leakeyi sp. nov.

FIG. 1. Astragalus and calcaneum sin., no. 2, R.1, 1947, anterior view. ×$\frac{2}{3}$.

Dicerorhinus or ***Aceratherium*** sp.

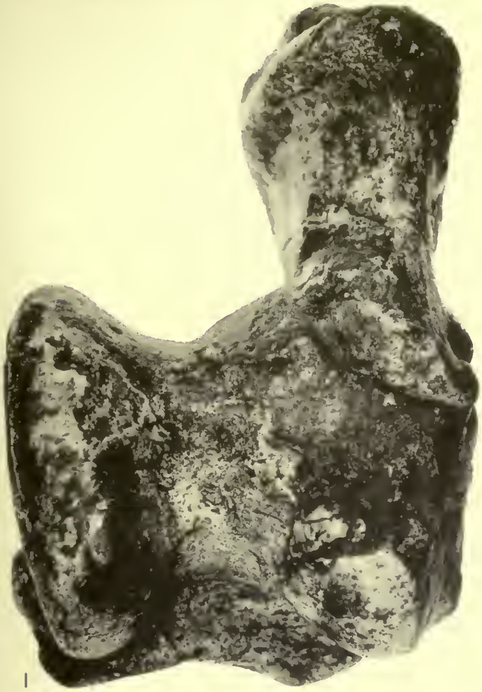
FIG. 2. Astragalus sin., Aloir, 1939, anterior view. ×$\frac{2}{3}$.
FIG. 6. Scaphoid sin., M.18897, Karungu, anterior view. ×$\frac{2}{3}$.
FIG. 7. Unciform sin., M.25191, Kathwanga, Rusinga, anterior view. ×$\frac{2}{3}$.

Brachypotherium heinzelini Hooijer

FIG. 3. Astragalus sin., no. 538, Gumba, Rusinga, 1949, anterior view. ×$\frac{2}{3}$.

Aceratherium acutirostratum (Deraniyagala)

FIG. 4. Scaphoid, lunar and cuneiform dext., no. 850, R.1, 1947, associated, anterior view. ×$\frac{2}{3}$.
FIG. 5. Same, proximal view. ×$\frac{2}{3}$.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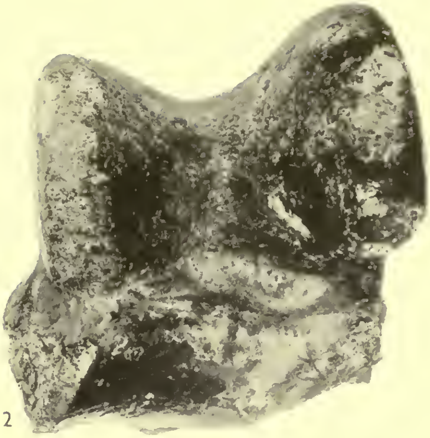
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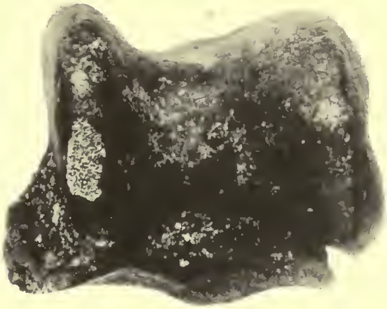
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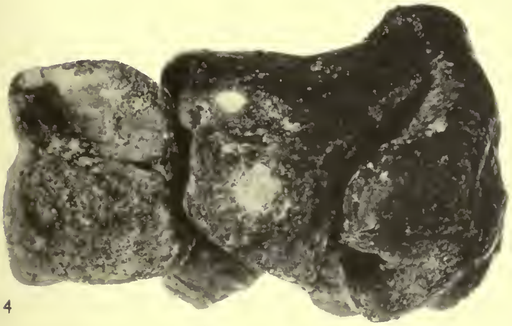
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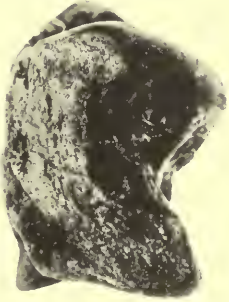
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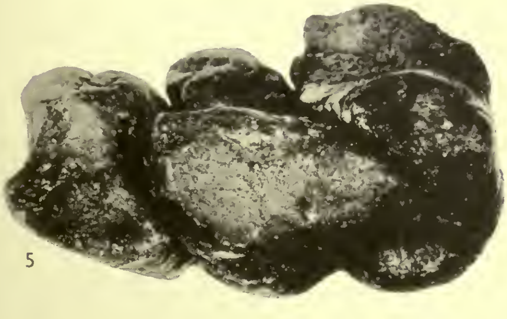
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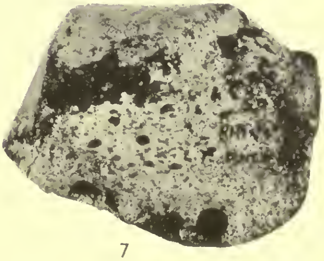
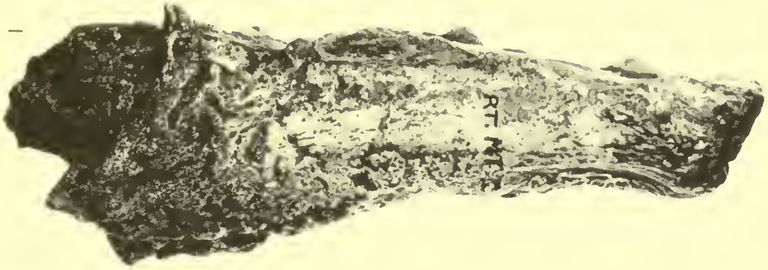

7

PLATE 15

Dicerorhinus leakeyi sp. nov.

FIG. 1. Diseased Mt. II dext., no. 2, R. 1, 1947, anterior view. ×⅗.
FIG. 2. Same, posterior view. ×⅗.
FIG. 3. Same, axial view. ×⅗.
FIG. 4. Normal Mt. II sin., no. 2, R. 1, 1947, axial view. ×⅗.

1



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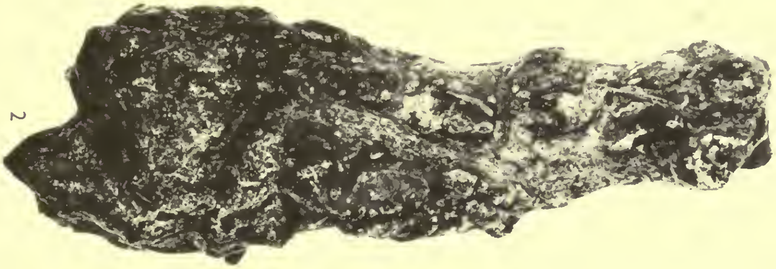

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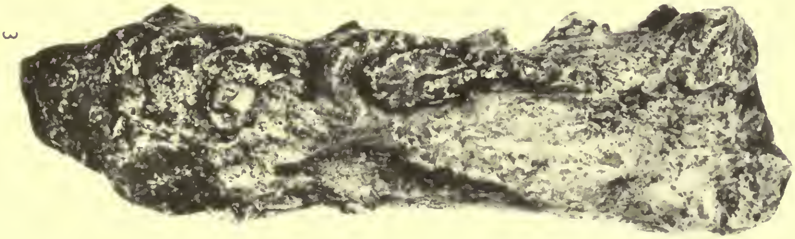

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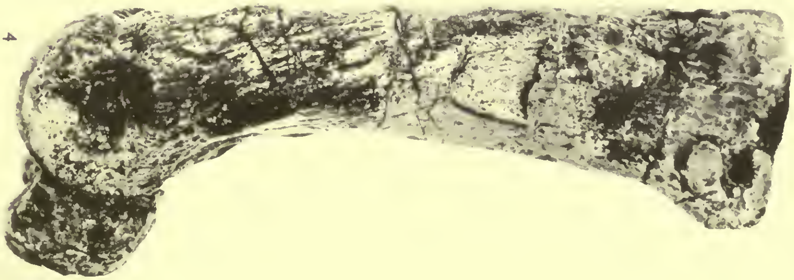

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THYSANOPELTIDAE (TRILOBITA) FROM THE BRITISH DEVONIAN

E. B. SELWOOD

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 13 No. 3
LONDON: 1966

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NATURAL HISTORY

THYSANOPELTIDAE (TRILOBITA) FROM THE BRITISH DEVONIAN

BY

EDWIN BRIAN SELWOOD, Ph.D.
University of Exeter

Pp. 191–220 ; 3 *Plates* ; 3 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 13 No. 3
LONDON : 1966

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THYSANOPELTIDAE (TRILOBITA) FROM THE BRITISH DEVONIAN

By E. B. SELWOOD

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SYNOPSIS

A revision of the British Devonian Thysanopeltidae is made and the following species described: *Scutellum* (*Scutellum*) *costatum costatum* Pusch, *S.* (*Scutellum*) *costatum whidbornei* subsp. n., *S.* (*Scutellum*) *costatum lummatonensis* subsp. n., *S.* (*Scutellum*) *delicatum delicatum* (Whidborne), *S.* (*Scutellum*) *delicatum tigrinum* (Whidborne), *S.* (*Scutellum*) *pardalios* (Whidborne), *S.* (*Scutellum*) *flabelliferum* (Goldfuss).

With the exception of *S.* (*Scutellum*) *costatum costatum*, which is known only from Upper Devonian localities, and *S.* (*Scutellum*) *flabelliferum*, which is of Upper Couvinian age, the fauna comes principally from two localities of Givetian age, namely Wolborough Quarry (Zone of *Maenioceras molarium*), near Newton Abbot, and Lummaton Quarry (Zone of *Maenioceras terebratum*), Torquay. The Givetian material is abundant and shows considerable variability; this is described and the evidence suggests that the species represented are closely related. Two lineages are recognized within the variants of both *S.* (*Scutellum*) *costatum* and *S.* (*Scutellum*) *delicatum* from the Middle Devonian; these are distinguished by separate subspecific names.

I. INTRODUCTION

Thysanopeltid trilobites from the Middle Devonian were first noted by Phillips (1841), who referred specimens from " Newton " to *Bronteus flabellifer* Goldfuss. Later, in a major study of the Devonian faunas, Whidborne (1889*a*) included details of all species and localities then known. From material assembled principally from Chercombe Bridge and Wolborough, near Newton Abbot, and Lummaton, near Torquay, he recognized six species of which three (*Bronteus pardalios*, *B. tigrinus*, and *B. delicatus*) were new. Passing reference to Whidborne's work has been made in a number of publications on Continental faunas, but, so far as is known, no specimens have been held to be conspecific with his species. Additional records of *Bronteus* are included in the Newton Abbot Memoir of the Geological Survey (Ussher 1913).

With the exception of *Scutellum alutaceum* (Goldfuss), which is not well established, the present investigation has confirmed the diversity of species noted by Whidborne.

At the same time, it is evident that Whidborne only selected for description certain specimens which could be readily distinguished from species established earlier, and by no means fully described the variability of each species. Sufficient material is now available to permit a quantitative investigation of the variation, and the species from Devonshire are here redescribed in the light of this variation.

The terminology employed is essentially that used in the *Treatise of Invertebrate Paleontology,* (*O*) *Arthropoda* 1, but is also supplemented by that of Šnajdr (1960). The latter work (an account of the thysanopeltid fauna of Bohemia) includes an interpretation and terminology of the lateral glabellar markings, which differs from that given by R. & E. Richter and used in the *Treatise.* Šnajdr's interpretation is based primarily on the nature and evolution of the muscle impressions seen on the inner surface of the exoskeleton beneath the glabellar furrows. These details cannot be recognized on the material described, but the interpretation appears well founded and is followed here. Studies of the British material suggest that the broad (*sag.*) occipital furrow, which is common within the Thysanopeltidae, is double and contains a preoccipital glabellar lobe. This, with its implication of a hitherto unrecognized glabellar furrow, further complicates the terminological difficulties. The nomenclature for the glabellar furrows is set out below.

Richter	Šnajdr	This paper
3p	3g	4p
Supplementary groove	2g	3p
2p	1g	2p
1p		
—	—	1p (preoccipital glabellar furrow)

II. ACKNOWLEDGMENTS

I wish to thank particularly Dr. W. T. Dean, Dr. R. Goldring, and Professor S. Simpson, who read and criticized the original manuscript, and Mr. J. Saunders, technician in the Department of Geology at Exeter, who is responsible for the photographs. Dr. V. Loudon and Dr. M. Stone offered helpful advice on statistical problems.

Dr. R. C. Blackie (Royal Albert Memorial Museum, Exeter), Mr. A. G. Brighton (Sedgwick Museum, Cambridge), Dr. M. L. K. Curtis (City Museum, Bristol), Dr. W. T. Dean (British Museum (Natural History)), Dr. R. J. G. Savage (Geology Museum, Bristol University) and Dr. F. S. Wallis (Torquay Natural History Museum) kindly permitted the examination and arranged the loan of specimens in their care.

III. OCCURRENCE AND RANGE

The provenance of much of the museum material is incomplete and frequently ambiguous. However, almost certainly only four main localities are involved: Wolborough Quarry and Chercombe Bridge Quarry near Newton Abbot, and Lummaton Quarry and Barton Quarry now within Torquay. In each town confusion arises because of the close proximity of the quarries and by the application of a variety of names, some of which have fallen into disuse, and others which have no precise geographical location. The principal alternatives and grid references are noted below.

1. Wolborough Quarry (SX852705): Woolborough, Wolvery, Newton Abbot, Newton, Newton Bushell, Woolbury.
2. Chercombe Bridge Quarry (SX832711): Chircombe, Cherecombe, Bradley Woods, Newton Bushell.
3. Lummaton Quarry (SX914665): Happaway, St. Mary Church, Babbacombe, Lummaton-Barton.
4. Barton Quarry (SX913671): No alternatives appear to be used.

Only two species of thysanopeltid trilobite recorded from South West England, *Scutellum flabelliferum* (Goldfuss) and *Scutellum costatum* Pusch, occur outside Britain. The former, which is characteristic of the Couvinian on the Continent, has only been identified positively by rare occurrences at Chercombe Bridge, probably from an horizon near to the Givetian/Couvinian boundary (Selwood 1965). This species represents the earliest thysanopeltid trilobite so far recognized from the British Devonian. *Scutellum costatum*, which has been recovered in considerable numbers from Wolborough, Lummaton and Barton, is relatively long ranging and continues both in Continental and British successions from the Givetian to the lower part of the Upper Devonian (*Manticoceras* Stufe). This particular species shows considerable variability and it has been found that forms closest to the original figures and descriptions are rare and recorded only from localities of Upper Devonian age (notably Ransleigh Quarry, near East Ogwell), whereas variants of the species from the Givetian at Lummaton and Wolborough are distinctive and referred to separate subspecies.

The British species of *Scutellum* are all of Givetian age, and occur within the Shell-Bed at Lummaton. The age of the Shell-Bed has been discussed by House (1963), who refers the horizon to the zone of *Maenioceras terebratum*. However, it seems that goniatites have not been identified positively from the Shell-Bed: recent collecting indicates that goniatites characteristically occur in a black bituminous bedded limestone, which appears as a faulted wedge in the quarry. Since these limestones, as well as the Shell-Bed, have yielded *Scutellum costatum lummatonensis* and *Scutellum costatum whidbornei*, there is some presumptive evidence for the contemporaneity of the two lithologies.

With the exception of *Scutellum delicatum tigrinum*, which has not been recognized, museum collections from Wolborough contain an identical thysanopeltid fauna to that from Lummaton. This particular locality has yielded goniatites (House 1963) indicating a lower horizon in the Givetian and referred to the zone of *Maenioceras molarium*.

IV. VARIABILITY

Scutellum occurs more commonly than any other trilobite in the British Middle Devonian, and museum collections contain large numbers of specimens. Within

TABLE I

		GIVETIAN			FRASNIAN	
	COUVINIAN	*C. cuspiforme*	*M. molarium*	*M. terebratum*	*P. lunulicosta*	*M. cordatum*
S. (*Scutellum*) *costatum costatum*	..	..	..	..	×	..
S. (*Scutellum*) *costatum lummatonensis*	..	..	×	×	..	..
S. (*Scutellum*) *costatum whidbornei*	..	..	×	×	..	..
S. (*Scutellum*) *delicatum delicatum*	..	..	×	×	..	..
S. (*Scutellum*) *delicatum tigrinum*	..	..	..	×	..	..
S. (*Scutellum*) *pardalios*	..	..	×	×	..	..
S. (*Scutellum*) *flabelliferum*	×	..	..	..	..	..
	Chercombe Bridge Limestone	?	Wolborough Limestone	Lummaton Limestone	Ransleigh Limestone	

Zonal range of the limestones based principally on House (1963). Possible gaps and duplications in the succession are not represented.

these collections pygidia predominate, and undoubtedly this bias reflects the relative prominence of pygidia during collection. The broad pygidia cause the rock to split readily to reveal complete specimens, whereas the more strongly vaulted cranidia and free cheeks are seldom found associated, and invariably need considerable preparation before being completely exposed.

Within the fauna, two distinct groups may be recognized: one in which the body is generally flattened and shows prominent, deeply impressed furrows on both the cranidium and pygidium, and another in which the body is highly vaulted and shows less prominent and less deeply impressed furrows. These two groups correspond in many ways to the *paliferum* and *companiferum* types of body plan described by R. & E. Richter (1934) but differ particularly in that the exoskeleton of the highly vaulted forms is neither greatly thicker than the flattened forms nor completely lacking in coarse ornamentation. The *paliferum* and *companiferum* groups are now considered to belong to different subgenera, but no such separation can be effected with the British material. Both types of body plan may be recognized amongst the variants of *Scutellum* (*Scutellum*) *costatum lummatonensis* subsp. n. and *S.* (*Scutellum*) *costatum whidbornei* subsp. n., and as such probably represent different adaptive forms within the species.

In addition to the variability noted above, it is clear from the large number of pygidia which has been assembled that there is, within each species, considerable

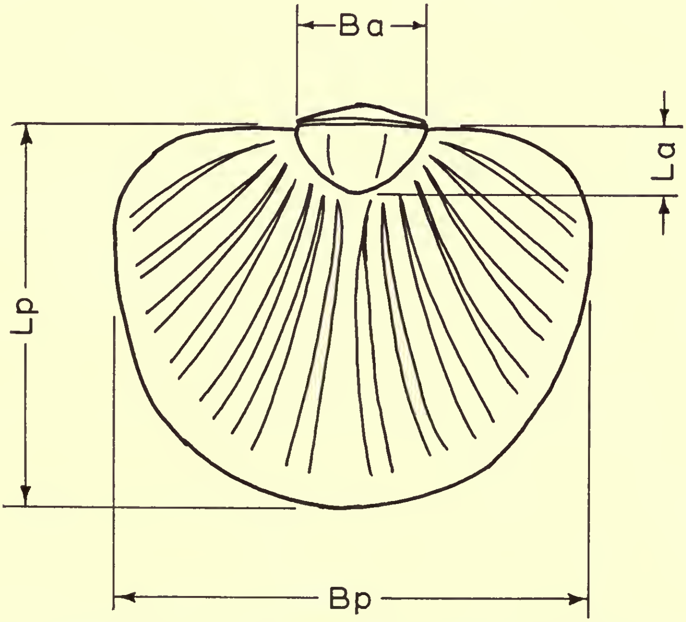
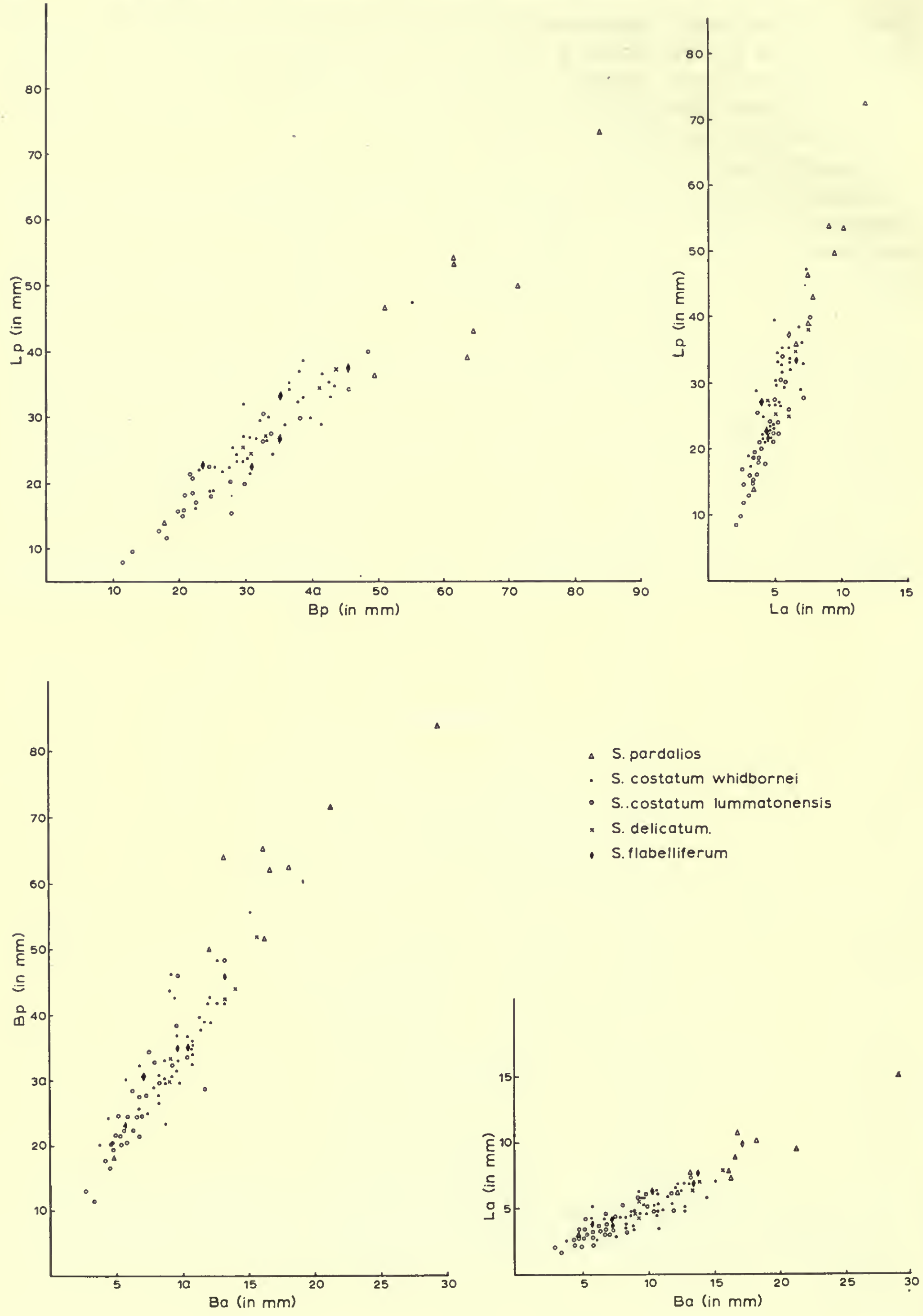


FIG. 1. Standard measurements of pygidium. *Bp*, breadth of pygidium; *Ba*, breadth of axis; *Lp*, length of pygidium; *La*, length of axis. The length measurements do not include the articulating half-ring, since this delicate structure is frequently not preserved.


Lp (in mm)
10
20
30
40
50
60
70
80
Bp (in mm)
10
20
30
40
50
60
70
80
90
Lp (in mm)
10
20
30
40
50
60
70
80
La (in mm)
5
10
15
Bp (in mm)
10
20
30
40
50
60
70
80
Ba (in mm)
5
10
15
20
25
30
▲ S. pardalios
• S. costatum whidbornei
○ S..costatum lummatonensis
× S. delicatum.
♦ S. flabelliferum
La (in mm)
5
10
15
Ba (in mm)
5
10
15
20
25
30

variability of morphological features. This variability is continuous within each species recognized and extreme variants are not referred to different species.

Within the total assemblage, specimens referred to *Scutellum costatum* far outnumber all others, and when the detailed characteristics of the pygidia are examined three important trends can be recognized from a norm close to *Scutellum costatum s. str.* which lead to diverse end members. These trends may be summarized as:

(i) Trend A, which is marked by a progressive increase in prominence of the median rib and a widening of the intercostal furrows (Pl. 2, fig. 9). These specimens have affinities with *Scutellum flabelliferum.*

(ii) Trend B, in which a progressive vaulting of the dorsal exoskeleton of the pygidium is accompanied by a weakening of the intercostal furrows (Pl. 2, figs. 11, 12, 15, 16). End members are thus close to *Scutellum pardalios.*

(iii) Trend C. This is less distinctive than trends A and B, but includes a range of specimens having affinities with *Scutellum delicatum.* These specimens show an increasing prominence of the median rib but no increase in the width of the intercostal furrows.

The range in variation from specimens near to *Scutellum flabelliferum* (Trend A) through the norm to the highly vaulted forms (Trend B) is paralleled exactly by previously undescribed material in which the ribs and axes are smooth or ornamented by widely spaced granules clearly visible only under a microscope. In order to distinguish between the two lineages, the smooth range of specimens has been referred to a new subspecies, *Scutellum costatum lummatonensis*, and since none of the granulated specimens corresponds in all respects to the characteristic material described by R. & E. Richter (1926) from the Upper Devonian of Germany, these are also referred to a new subspecies, *Scutellum costatum whidbornei.*

Scatter diagrams (Text-fig. 2) relating the length of the standard measurements (Text-fig. 1) of *Scutellum costatum* show on arithmetic coordinates a markedly rectilinear distribution. This feature suggests that only a single species is present which, in the size range represented, shows isometric growth. Specimens referred to *Scutellum costatum whidbornei* are distinguished on the scatters from the subspecies *Scutellum costatum lummatonensis* and it is apparent that, whilst representatives of both subspecies are distributed throughout the range of scatters, specimens referred to *Scutellum costatum lummatonensis* are generally smaller than those of *Scutellum costatum whidbornei.* The reduced major axis has been calculated for the pairs of variables shown in Table II, and the results obtained for each subspecies compared (see Miller & Kahn 1962 : 205) by calculating the statistic Z for each pair of growth indices and referring to tables of Z which give the areas under the normal probability curve. The differences between the growth indices are not significant ($P = 0{\cdot}05$), so that the calculation fails to disprove the hypothesis tested; namely that the difference between growth indices is no greater than would be expected by drawing two random samples from the same normal population.

FIG. 2. Scatter diagrams showing variation within British thysanopeltid trilobites.

TABLE II

		R.M.A.	St. Error of slope	St. Error of intercept	Dispersion around R.M.A.	Correlation coefficient	Number of specimens	Comparison of growth indices Z	Comparison of growth indices Probability
Bp/Lp	a	$y = 0{\cdot}83x - 1{\cdot}14$	0·177	0·926	6·423	0·994	27	0·483	>0·05
	b	$y = 0{\cdot}92x + 2{\cdot}13$	0·016	0·850	5·487	0·995	32		
Ba/Bp	a	$y = 3{\cdot}46x + 2{\cdot}13$	0·098	1·504	7·426	0·988	30	0·054	>0·05
	b	$y = 3{\cdot}47x + 0{\cdot}05$	0·077	1·395	5·981	0·991	35		
La/Lp	a	$y = 5{\cdot}56x + 1{\cdot}35$	0·115	0·912	3·564	0·994	29	1·248	>0·05
	b	$y = 5{\cdot}30x + 1{\cdot}97$	0·176	1·755	9·144	0·980	35		
Ba/La	a	$y = 0{\cdot}51x + 0{\cdot}33$	0·013	0·213	2·413	0·998	33	0·479	>0·05
	b	$y = 0{\cdot}46x + 0{\cdot}48$	0·012	0·226	2·804	0·986	39		

a. *Scutellum* (*Scutellum*) *costatum lummatonensis*.
b. *Scutellum* (*Scutellum*) *costatum whidbornei*.

TABLE III

	R.M.A.	St. Error of slope	St. Error of intercept	Dispersion around R.M.A.	Correlation coefficient	Number of specimens	
Bp/Lp	$y = 0·89x - 2·35$	0·122	0·090	9·531	0·994	59	*S. costatum whidbornei* and *S. costatum lummatonensis*
Ba/Bp	$y = 3·33x + 2·15$	0·059	1·397	10·953	0·989	65	
La/Lp	$y = 5·62x - 0·55$	0·124	1·515	11·411	0·984	64	
Ba/La	$y = 0·51x + 2·19$	0·010	0·235	4·10	0·986	72	
Bp/Lp	$y = 0·87x - 5·75$	0·395	3·092	9·361	0·991	9	*S. pardalios*
Ba/Bp	$y = 2·75x + 12·73$	0·139	3·857	8·368	0·988	9	
La/Lp	$y = 5·04x - 11·78$	0·141	1·737	3·871	0·996	9	
Ba/La	$y = 0·49x + 0·46$	0·173	0·436	2·336	0·994	10	
Bp/Lp	$y = 0·90x - 2·64$	0·098	0·169	0·425	0·999	5	*S. delicatum*
Ba/Bp	$y = 1·91x + 16·34$	0·035	0·011	0·518	0·999	5	
La/Lp	$y = 4·76x + 1·71$	0·699	4·452	1·167	0·994	5	
Ba/La	$y = 0·46x + 0·67$	0·032	0·218	0·611	0·996	6	
Bp/Lp	$y = 0·81x + 0·57$	0·035	1·322	2·014	0·995	5	*S. flabelliferum*
Ba/Bp	$y = 2·70x + 9·93$	1·566	1·707	2·269	0·991	5	
La/Lp	$y = 4·52x + 5·27$	0·178	1·583	1·206	0·996	5	
Ba/La	$y = 0·57x + 0·31$	0·012	0·795	0·670	0·998	7	

Data pertaining to the other species from South West England have been added to the variation diagrams (Text-fig. 2); for the most part the specimens concerned either fall within, or from a natural extension of, the scatters of *Scutellum costatum*. Thus, on the basis of the measured characters, a close relationship is indicated between the species, but as a complete gradation of characters used in the original diagnoses of the species has not yet been observed, it is not permissible to conclude that the whole fauna forms part of a single species. To facilitate the comparison of the measured characters the reduced major axes of *Scutellum costatum lummatonensis* and *S. costatum whidbornei* have been recalculated as a single population and the results included in Table III together with those for *Scutellum delicatum*, *S. flabelliferum* and *S. pardalios*. When comparisons are made with *Scutellum costatum*, according to the method noted above, the results (Table IV) indicate significant ($P = 0{\cdot}05$) differences between certain pairs of growth indices. These results do not immediately mark out certain species as being similar to or different from *Scutellum costatum*, but *Scutellum delicatum*, in which only one ratio is significantly different, appears more closely related to *Scutellum costatum* than to *Scutellum pardalios* in which three of the four ratios compared are significantly different. This is in part confirmed by an inspection of other unmeasured characters, for whereas *Scutellum costatum* shows a trend towards *Scutellum delicatum*, and *Scutellum delicatum* shows both smooth and granulate forms, *Scutellum pardalios* shows limited variability only.

TABLE IV

	S. costatum/S. pardalios		*S. costatum/S. delicatum*		*S. costatum/S. flabelliferum*	
	Z	*P*	*Z*	*P*	*Z*	*P*
Bp/Lp	0·042	>0·05	0·032	>0·05	0·599	>0·05
Ba/Bp	3·861	<0·01	20·469	<0·01	0·403	>0·05
La/Lp	3·117	<0·01	1·213	>0·05	5·070	<0·01
Ba/La	8·245	<0·01	1·327	>0·05	1·851	>0·05

Scutellum flabelliferum is stratigraphically older than the other species but three of the four growth indices are not significantly different from those of *Scutellum costatum*. In some specimens the median rib is reduced in size and this suggests that the species could provide a range of variation from which *Scutellum costatum* could have been derived.

These comparisons thus broadly confirm the close relationship which was suggested to exist between *Scutellum costatum* and *Scutellum delicatum* and *Scutellum flabelliferum* but they do suggest that *Scutellum pardalios* is distinct. It should be remembered however that that the reduced major axes of species other than *Scutellum costatum* are based on relatively few specimens so that the calculated probabilities could well be underestimated.

V. ECOLOGY

The significance of the *paliferum* and *companiferum* types of body plan has been discussed at some length by R. & E. Richter (Richter, R. 1926; Richter, R. & E. 1934), who interpret certain structural elements as strengthening mechanisms for the exoskeleton. Whilst these two types are not recognizable precisely in the terms defined by Richter within the British material, both highly vaulted and flattened forms do occur (p. 197) and these appear to have ecological significance.

In all thysanopletid trilobites the pygidium is the most prominent part of the exoskeleton, commonly equalling half the length of the body, and undoubtedly the distinctive shield-like form had considerable adaptive significance. This is confirmed by the exceptional amount of diversification within the group. The thin delicate dorsal exoskeleton, the high proportion of surface area to body volume, and the distribution of individuals through a wide range of lithologies, suggest that the flattened forms were active and free-swimming. In complete specimens it is not uncommon to find the thorax flexed so that the pygidium and cephalon are inclined in opposite directions, either upwards or downwards. Whilst this could be a *post mortem* phenomenon it is possible that swimming was aided by paddle-like movements of the pygidium. The effect of such movements would be enhanced by the considerable expansion of the pleural region. The small size of the axis and the considerable breadth of the doublure indicate that the pygidial appendages were most probably reduced; this might be expected if the swimming function had been, in part, taken over by the action of the whole pygidium. Such a reduction of the appendages would seemingly affect the efficiency of the respiratory system, but this could well be offset by direct diffusion of gases in solution through the thin integument.

The strongly vaulted forms are more robust and not so clearly adapted for active swimming. Without exception, they are all restricted to the Shell-Bed lithology at Lummaton and Wolborough, which has been interpreted by Elliot (1961) and Dineley (1961) as shell débris infillings of original depressions on a stromatoporoid reef. They may well have lived actually browsing on the reef.

VI. DETERIORATION OF THE BASAL PART OF THE GLABELLA

Within the Thysanopeltidae the " occipital furrow " is normally broad (*sag.*), deeply convex and frequently marked at the lateral extremities by tumour-like swellings. In the native British species the furrow is more deeply excavated at its anterior and posterior limits, and in *Scutellum pardalios* it shows a moderately elevated band within the furrow. This band together with the tumour-like swellings are coarsely ornamented. The presence of ornamentation within the cranidial furrows is unknown and suggests that a preoccipital glabellar lobe is present, which is divided into median and lateral lobes (the latter being represented by the tumour-like swellings). Thus the anterior excavation of the " occipital furrow " would appear to represent a transverse preoccipital glabellar furrow, the ornamented section the preoccipital glabellar lobe, and the posterior groove the true occipital furrow.

Although Whidborne fully described the character of the " occipital furrow " in his original description of *Scutellum pardalios*, no significance was attached to it by him or by later authors. A somewhat similar arrangement is also indicated in *Scutellum alutaceum geesensis* (see Richter, R. & E. 1956, pl. 7, fig. 44A) but no comment has been offered. The present interpretation, affecting as it does the nature of the segmentation of the cephalon must be of significance and be represented in all members of the family. It is interesting to note that *Eobronteus* (Text-fig. 3A), which is usually considered to be close to the origin of the family, shows a narrow occipital furrow and, in addition, the base of the glabella is weakly constricted at its lateral margin. The latter could well indicate the presence of the basal glabellar lobe which was reduced in the course of evolution.

It is suggested therefore that the broad " occipital furrow " which is usual in the family, has a composite structure formed through the disappearance of the preoccipital glabellar lobes and the coalescence of the preoccipital glabellar furrow and occipital furrow. Where the tumour-like swellings occur, it may be interpreted that the median glabellar lobe only has been lost.

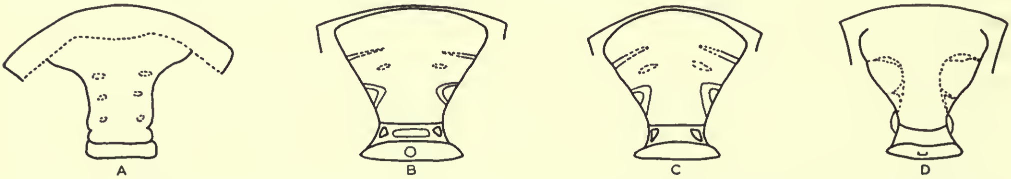


Fig. 3. Deterioration in the basal part of the glabella in the Thysanopeltidae. A, *Eobronteus laticauda* (Wahlenberg). Upper Ordovician. Occipital furrow narrow, 1p indicated at the axial furrow ; B, *Scutellum* (*Scutellum*) *pardalios* (Whidborne). Middle Devonian. 1p transglabellar, preoccipital ring divided into three small lobes ; C, *Scutellum* (*Scutellum*) *delicatum* (Whidborne). Middle Devonian. 1p transglabellar, median lobe of preoccipital ring absent ; D, *Scutellum* (*Thysanopeltis*) *speciosum* (Hawle & Corda). Middle Devonian. Preoccipital lobes absent, a coalesced groove area only is left. (Figs. A and D after R. & E. Richter 1956).

Thus it appears that there is, within the Thysanopeltidae a deterioration of the basal part of the glabella which is quite comparable to that seen in the Phacopidae and the Proetidae (Richter, R. & E. 1939). Text-fig. 3 illustrates the principal modifications of the basal part of the glabella seen in the family ; the specimens are arranged in a morphological series but this is not intended to imply stratigraphical or evolutionary significance.

VII. SYSTEMATIC DESCRIPTIONS

Family **THYSANOPELTIDAE** Hawle & Corda 1847

Genus ***SCUTELLUM*** Pusch 1833

Type species. *Scutellum costatum* Pusch 1833.

Scutellum* (*Scutellum*) *pardalios (Whidborne)

(Pl. 1, figs. 1–11)

1889 *Bronteus pardalios* Whidborne : 29.
1889*a* *Bronteus pardalios* Whidborne ; Whidborne : 35, pl. 3, figs. 1–7.

Type locality. Wolborough Quarry (SX852705) near Newton Abbot, Devon.

HORIZON. Middle Devonian. Givetian. Zone of *Maenioceras molarium* (Wolborough Quarry) and of *M. terebratum* (Lummaton Quarry).

LECTOTYPE. Here selected BM I.100. A pygidium figured by Whidborne (1889*a*, pl. 3, fig. 5). This figure represents a restored specimen; the original is refigured (pl. 1, figs. 1–3).

SYNTYPES. SMC H.4,108–113. BM In.34924.

FIGURED SPECIMENS. BM IT.495 (Pl. 1, figs. 4, 5); BM IT.496 (Pl. 1, fig. 6); SMC H.4,112 (Pl. 1, fig. 7); RAMME 7149 (Pl. 1, figs. 8–11).

MEASUREMENTS OF LECTOTYPE (in mm.)

Length of pygidium	73·0	Length of axis	15·0
Breadth of pygidium	84·0	Breadth of axis	29·5

DIAGNOSIS. A species of *Scutellum* (*Scutellum*) showing a highly vaulted, but thin, dorsal exoskeleton. Furrows, of both cranidium and pygidium less prominent and less deeply impressed than usual for subgenus. Ornament consisting of coarse, closely spaced tuberculation. On pygidium and more sporadically on cephalon, ornament developed as prominent hollow truncated cones. Median and lateral preoccipital glabellar lobes raised and ornamented. Occipital ring ornamented by a massive mesial spine.

DESCRIPTION

In plan the glabella is broader than it is long, and expands forward rapidly to reach a maximum breadth (2·5 times greater than at the posterior) just short of the anterior margin of the cranidium. The anterior margin of the glabella forms a broad arc which at the sagittal line extends to the anterior border. The glabellar furrows are not prominent. 4p is short, transverse and only recognizable at the lateral margin of the glabella. It deepens towards the axial furrow and is placed one-third of the distance from the anterior margin of the glabella to the preoccipital glabellar lobe. 3p is frequently scarcely recognizable, but is sometimes seen as a small transversely elliptical depression lying midway between the axial furrow and the sagittal line at a position half way between 4p and 2p. 2p is broader and more prominent than the glabellar furrows to the anterior. It is horseshoe-shaped and is marginally placed on the glabella so that the anterior and posterior branches run into the axial furrow. That part of the glabella so isolated forms a prominent node. The posterior branch is more deeply impressed than the anterior. The preoccipital furrow (1p) is transglabellar, broad (*sag.*) and deeply impressed and curves gently towards the anterior distally. It shows a symmetrical cross-section. The occipital furrow is less deeply impressed and shows an asymmetrical cross-section, rising more steeply to the anterior than to the posterior. The preoccipital glabellar lobe is low; the median lobe is isolated and forms a narrow flat band, but the lateral lobes are more strongly elevated and recognizable as swellings arranged oblique to the preoccipital furrow. The glabella is defined by deeply impressed axial furrows; the section that lies posterior to 2p is short and almost parallel to the sagittal line;

it then curves sharply outwards at the occipital furrow, thus considerably increasing the breadth (*trans.*) of the occipital ring. The section of the axial furrow anterior to 2p diverges from the sagittal line at approximately 45° ; it is less deeply impressed than the posterior section and deepens towards a pit, obliquely placed across the furrow, which is positioned adjacent to glabellar furrow 4p. The occipital ring is prominent and broad, reaching half the maximum breadth of the glabella ; it is characterized by a prominent backwardly-directed mesial tubercle. The frontal area of the cranidium is small and only recognizable as slightly flattened areas situated at the anterior lateral extremities of the glabella. The anterior border furrow is weak and clearly defined only away from the sagittal line. The anterior border is narrow and shows a more or less level surface ornamented by 2–3 continuous terrace lines. From the anterior margin it is recurved sharply to the posterior ; this section is ornamented by 3–4 continuous terrace lines. At the antero-lateral margin of the cranidium this border is strongly upstanding but it is scarcely raised at the sagittal line. The fixed cheeks are large and inflated, and attain their maximum breadth posteriorly, but narrow rapidly anteriorly between the facial suture and the axial furrows. From the highest part of the fixed cheek, the cheek area falls away steeply to the posterior but more gently to the anterior. The posterior border furrow of the cranidium is positioned close to the margin. From its origin which is just removed from the axial furrow, it runs obliquely towards the anterior, making an angle of approximately 20° with the posterior border. In this section the furrow has a sharp V-shaped cross-section. At a point below the palpebral lobe the furrow turns posteriorly to run more or less parallel to the facial suture ; in this section the furrow has a broad evenly rounded cross-section. Posteriorly the furrow narrows and fails to reach the posterior margin. This furrow is not observed in the librigenae. The posterior border forms a flattened plane sloping towards the posterior border furrow ; from its origin near the glabella it widens rapidly distally. The palpebral lobe is small and semicircular in outline ; its anterior lies opposite 2p and its posterior is positioned opposite the posterior end of the glabella. The palpebral lobe is placed farther from the sagittal line than the anterior lateral border of the cranidium. The palpebral furrow forms a shallow open groove ; it has not been traced beyond the anterior limit of the lobe but continues posteriorly, progressively shallowing, following a course broadly parallel to the posterior branch of the facial suture for about one-third of the length of the latter. The anterior branch of the facial suture is long and gradually approaches the axial furrow towards the anterior. From the palpebral lobe this branch diverges outwards at approximately 10° from the exsagittal line ; opposite 3p it swings inwards but then almost immediately resumes its course to the anterior and runs more or less parallel to the sagittal line, finally cutting the anterior margin of the cephalon almost at right angles. The posterior branch of the facial suture is short, from the posterior end of the palpebral lobe it swings outwards through a semicircle to run almost parallel to the posterior border. It then curves sharply to the posterior to cut the posterior border obliquely at a distance from the axial furrow equal to four-fifths of the breadth (*trans.*) of the occipital ring.

The frontal profile is made up of 5 prominent and distinct arches comprising the central glabella, bounded by the fixed cheeks and the palpebral lobes. The glabella is strongly inflated and subtriangular in outline and its sides decline from the crest at approximately 60°. The crestal point, at the sagittal line, is rounded and lies well above the adjoining parts of the fixed cheeks. Deeply incised axial furrows separate the glabella from the fixed cheeks; these have an open V-shaped cross-section. Each fixed cheek is bounded adaxially by the axial furrow and abaxially by the palpebral furrow. The highest part of the cheek area is rounded and lies three-quarters of the distance from the axial furrow to the palpebral furrow. From this point the cheeks slope down to the axial furrow at approximately 60° and rather more gently to the palpebral furrow. The palpebral lobe is flat or gently inclined towards the weakly impressed palpebral furrow.

In side view the glabella is strongly inflated and stands well above the adjoining parts of the cranidium. It rises steeply from the preoccipital furrow and then slopes more gently to a crestal point one-third the distance from the preoccipital furrow to the anterior border. The anterior section of the curve slopes gently to the anterior but steepens up at the anterior border furrow. No preglabellar field is seen. The border furrow is evenly concave and rises anteriorly into a low insignificant border. The preoccipital furrow is relatively long (*sag.*) and deep and passes into a low evenly inflated median preoccipital lobe. The occipital furrow is narrower and less deeply impressed than the preoccipital furrow. The occipital ring is asymmetrical and rises almost vertically from the posterior to the crestal point, which approximates to the level of the base of the glabella; it then slopes more gently to the occipital furrow. The preoccipital ring is about one-third of the length (*sag.*) of the occipital ring.

The free cheek is of moderately large size and is subtriangular in outline. The eye is prominent and strongly curved longitudinally and is seen to occupy the highest part of the free cheek but lies below the level of the palpebral lobe. The eye surface is convex, directed upwards and outwards, and marked by numerous holochroal facets which give a machine turned appearance to the surface. A prominent evenly rounded eye socle separates the eye from the rest of the free cheek. The cheek area is longer than broad and slopes steeply away from the eye to a broad, concave furrow which bounds the lateral part of the cheek. Towards the anterior, the cheek area slopes more gently than laterally. The border is small and appears as a narrow rim to the cheek ornamented by discontinuous raised lines directed obliquely backwards.

In plan the pygidium is semielliptical in outline and broader than long, with a length : breadth ratio of 5 : 7; the maximum breadth is attained just posterior to the axis. The articulating half-ring is small, delicate and broadly curved. The articulating ledge which forms the inner part of the anterior margin is straight and measures three-fifths of the maximum pygidial breadth. This ledge terminates in a small articulating wing; from this point the outer part of the anterior margin curves in an even arc to the lateral margin of the pygidium. The axis is small and subtriangular. At the anterior margin its measurements exceed one-third of the maximum breadth recorded for the pygidium and at the sagittal line it approaches one-sixth of the total pygidial length. A broad, deep and evenly rounded furrow clearly separates the axis from the articulating half-ring. This furrow is divided into three equal sections by two weak constrictions marking longitudinal furrows which are continued into the axis and effect a weak trilobation. From the anterior margin of the axis these furrows are directed posteriorly parallel to the sagittal line. At a point half the distance (*exsag.*) from the anterior margin to the axial furrow, they curve evenly inwards so that the straight sections are united by an almost semicircular furrow which, at the median line, lies only one-sixth of the total distance from the posterior margin of the axis to the anterior. The median lobe of the axis is evenly inflated and the lateral lobes slope steeply to the pleural furrows. The axial furrows are broad, smooth, and particularly deeply set at the anterior margin. At the midpoint the axial furrows are constricted ; the posterior section of each furrow makes an angle of 40° with the sagittal line whilst the anterior section, if projected, would make an angle of 50°. No segmentation of the axis has been observed. The flanks of the pygidium are strongly vaulted. The inner part of the pleural region forms a pronounced elevated platform which, at the sagittal line, extends two-thirds of the distance from the axial furrow to the posterior margin. The outer boundary of the platform crosses the ribs at their midpoints to reach the anterior margin at the articulating wing. Broadly, the platform is at two levels for ribs 1–2 lie at a distinctly lower level than ribs 4–7 ; rib 3 occupies an intermediate position. The median rib lies in a weakly depressed position on the higher platform. From the margin of the platform, the pleurae slope steeply to the periphery of the pygidium. The pleural field is divided by narrow moderately impressed intercostal furrows into 7 paired ribs and a single medianly placed rib, which radiate out from the axis. The intercostal furrows weaken towards and fail to reach the axis and also stop short of the periphery of the pygidium. The first pair of intercostal furrows is more deeply impressed than the following, so that ribs 1 and 2, and particularly rib 1, are more convex than the succeeding ribs. The two anterior pairs of intercostal furrows are almost straight but towards the posterior the furrows become weakly S-shaped, each furrow curving weakly to the anterior at the margin of the pygidium. Each rib attains its maximum breadth at the periphery and decreases in breadth progressively towards the axis. The second pair of ribs tapers very strongly and barely reaches the axis. Ribs 3–6 are moderately broad at the axis (about one-third of the maximum peripheral breadth), but rib 7 and the median rib are narrower (about one-fifth of the maximum peripheral breadth). All of the ribs are broad and flattened at the periphery but increase in convexity progressively towards the platform. On the peripheral parts of the platform the ribs are moderately inflated but, with the exception of rib 1, all flatten somewhat as the axis is approached.

In side view the axis extends posteriorly for a quarter of the total sagittal length of the pygidium ; it is strongly delimited anteriorly from the articulating half-ring by a deep evenly curved furrow and posteriorly by a less prominent groove. The axis is strongly inflated, rising steeply from the articulating furrow but descending rather more gently to the posterior. The platform is very lightly and evenly bowed and extends posteriorly from the axis for a distance approaching two-thirds of the total post axial length (*sag.*). Posteriorly the platform passes gradually into a broadly concave slope which extends to the posterior margin of the pygidium.

Viewed from the posterior the axis occupies a prominent elevated position and appears weakly trilobed in outline. The evenly rounded median lobe of the axis passes gently into the more flattened lateral lobes ; the latter curve sharply down to deeply impressed pleural furrows. The outer section of the lateral lobe, the axial furrow, and the inner section of the anterior margin are obscured by the elevated posterior section of the pygidium, which rises in this view to a height approaching half that of the axis. The anterior pleural region is relatively low and weakly S-shaped and slopes gently to the outer margin.

The doublure is thin and is closely applied to, and follows the vaulting of, the dorsal exoskeleton. In the pygidium its inner margin reaches the platform. In the ventral view, the position of the intercostal furrows is marked by moderately convex elevations.

The anterior border of the cranidium is ornamented by 3–4 unbranched hair-like lines which run parallel to the margin of the cranidium. The posterior border of the fixed cheeks is smooth. The glabella is characterized by massive, pointed tubercles directed obliquely backwards. These tubercles, which are frequently broken, are smaller and more closely spaced towards the anterior, particularly on the median part of the glabella. Towards the posterior of the glabella the tubercles are prominent and frequently elongated transversely. In the posterior glabellar region a tubercle, larger than any of the others, lies on the sagittal line just anterior to the preoccipital furrow. Usually the occipital ring is broken medianly, but in perfect specimens it is characterized by a massive mesial tubercle which swells to occupy the whole length (*sag.*) of the ring. This tubercle is drawn out into a sturdy spine, directed obliquely backwards. The lateral parts of the ring are ornamented by small, irregular tubercles of which 2–3 would be encountered on an exsagittal traverse ; these tubercles are comparable in size to those at the anterior end of the glabella. The median lobe of the preoccipital ring is marked by two rows of small tubercles, and the lateral lobes show 2-3 tubercles of varying size. The fixed cheeks are tuberculate but with smaller tubercles than on the glabella ; these are of fairly uniform size but do increase in size slightly towards the palpebral lobe. The latter is also tuberculate and shows one particularly large tubercle on its posterior border. All of the furrows of the cranidium are smooth. The free cheek is ornamented by closely spaced tubercles comparable in size to those occurring on the outer parts of the fixed cheeks. These tubercles, which are almost invariably broken at their summits are directed obliquely backwards and become more closely spaced and regular in size towards the genal angle. Finer tubercles appear towards the borders.

The pleural region of the pygidium is bounded by a narrow margin which is ornamented by delicate hair-like lines ; at the anterior these lines run broadly parallel to the border but posteriorly lie oblique to the margin. The ribs and axis are covered with coarse, closely spaced tubercles which appear as truncated cones directed upwards and backwards. The larger tubercles, which approach 1 mm. in diameter at their summits in large specimens, tend to be more abundant towards the periphery of the pygidium and are irregularly associated with smaller tubercles. Across the ribs (*trans.*) some 6 tubercles are recorded at the periphery and two near the axis. Inevitably many of the tubercles are damaged in the course of collecting the specimens and this gives the impression that they represent the broken bases of delicate hollow spines. However, there is a remarkable uniformity in the heights of the tubercles, which would not necessarily be expected if spines were represented as a continuation of the dorsal exoskeleton. Further, it is evident from perfectly preserved tubercles that the exoskeleton is not broken at the summit of the cone but is recurved slightly to form a narrow flat ring surrounding a depressed central area which is marked by broken secondary calcite. Thus it is unlikely the dorsal exoskeleton was ever continued into prominent spines. All of the furrows of the pygidium are smooth. Sectioned material containing pygidia embedded in matrix has revealed the presence of exceedingly delicate setae, one of which fits into the central pit of each tubercle. These setae are hollow and now filled with fibrous calcite which is apparently continuous with the secondary calcite filling the body space between the dorsal exoskeleton and the doublure. It may be presumed that the setae were movable and responsive to tactile stimuli ; the extreme delicacy of the walls suggests that the setae may also have been the receptors of chemical stimuli.

The ventral surface of the doublure is ornamented by clear asymmetrical furrows which are continuous or occasionally branched and run more or less parallel to the border of the cephalon and pygidium. The furrows are crowded at the periphery but become gradually more widely spaced until at the inner margin the interval between them is six or seven times as great as at the periphery. On the dorsal surface of the doublure these furrows are represented as weakly raised areas.

STRUCTURE OF THE EXOSKELETON. All specimens possess, for their size, an exceedingly thin and delicate exoskeleton ; in a pygidium 40 mm. long the total thickness is only 0·09 mm. Sectioned material reveals that the exoskeleton is made up of three layers ; a thin outer (dorsal) layer, a middle layer 4 times as thick as the outer layer, and a thin inner layer twice as thick as the outer layer. The inner and outer layers are distinguished by being rather more heavily pigmented than the middle layer. This threefold division of the dorsal exoskeleton has been recorded in a number of other trilobites (Harrington 1959 : 85) ; in all cases the middle layer is the thickest but the relative thickness of the other layers varies. Since Kielan (1954) records that the outer layer is thicker than the inner layer in *Scutellum flabelliferum* it is evident that these relative thicknesses are not uniform for the genus.

On the cephalon the exoskeleton thins over the tubercles ; it has not been possible to determine whether all of the layers are represented here, but the thickness observed suggests that more than the outer layer is represented. It is unlikely that the mineralized exoskeleton was ever continuous over the tubercles on the pygidium (p. 210).

Considering the large size of this species and the thickness of the dorsal exoskeleton it is perhaps surprising that the specimens, particularly the pygidia, have survived intact. However, R. & E. Richter (1934) have pointed out the very considerable reinforcement given by the broad doublure closely applied to the dorsal exoskeleton ; this is supplemented in *Scutellum pardalios* by thickening of the exoskeleton in the narrow furrows. Thus, the highly vaulted pygidia are supported by thickened arches (intercostal furrows) which radiate out from the axis to the periphery. The size and the general absence of malformed specimens suggest that the exoskeleton was quite adequate for its functions. Where break up of the specimens has been observed it is quite clearly posthumous and results from the effects of either compaction or tectonic activity, and reflects not the fragile exoskeleton but the large area covered by each specimen. The minor displacements associated with the fracturing of the exoskeleton frequently give the impression that the exoskeleton is thick, for it reveals beneath the true exoskeleton layers of fibrous calcite which grew around the specimen during diagenesis and appear superficially as a continuation of the dorsal exoskeleton.

COMPARISONS. The character of the ornamentation serves to distinguish the species from all others in the subgenus *Scutellum* (*Scutellum*). Within this subgenus the pygidium is most closely related to the highly vaulted forms of *Scutellum* (*Scutellum*) *costatum whidbornei*, but is distinguished from it by its ornament, size, and by the narrower and less clearly impressed interpleural furrows. The glabella is broader and much more strongly vaulted than in *S.* (*Scutellum*) *costatum*.

Many of the features of this species are characteristic of the subgenus *S.* (*Paralejurus*) but it is distinguished from all members of this subgenus by the thin exoskeleton, the prominent ornamentation and by the more deeply impressed intercostal furrows of the pygidium.

Scutellum* (*Scutellum*) *costatum costatum Pusch

(Pl. 2, fig. 10)

1833 *Scutellum costatum* Pusch : 119.
1926 *Scutellum costatum* Pusch ; Richter, R. & E. : 117, pl. 7, figs. 18–23 (includes earlier synonymy of the species).
1954 *Scutellum* (*Scutellum*) *costatum* Pusch ; Kielan : 31.
1955 *Bronteus costatus* (Pusch) Maksimova : 32, pl. 1, figs. 5–9.
1956 *Scutellum* (*Scutellum*) *costatum* Pusch ; Richter, R. & E. : 96, 101, pl. 2, figs. 7, 8.

REMARKS. *Scutellum* (*Scutellum*) *costatum s. str.* is rare and has only been positively identified from horizons of Upper Devonian age in Devon (p. 195), and it appears to be the end member of a continuously varying series extending from the Lower Middle Devonian *Scutellum flabelliferum* through *Scutellum costatum whidbornei* subsp. n. in the Upper Middle Devonian. The possibility of such a relationship existing between *Scutellum flabelliferum* and *Scutellum costatum* was indicated by R. & E. Richter (1926 : 121).

FIGURED SPECIMEN. TM B.490 (Pl. 2, fig. 10).

Scutellum (*Scutellum*) *costatum whidbornei* subsp. n.

(Pl. 2, figs. 9, 11-18)

1861 *Bronteus flabellifer* Goldfuss ; Pengelly : 343, pl. 7, fig. 2.
1889*a* *Bronteus granulatus* Goldfuss ; Whidborne : 40, pl. 3, fig. 10.

Derivation of name. After the Rev. G. F. Whidborne.

Type locality. Wolborough Quarry (SX852705) near Newton Abbot, Devon.

Horizon. Middle Devonian. Givetian. Zone of *Maenioceras molarium* (Wolborough Quarry) and of *M. terebratum* (Lummaton Quarry).

Holotype. BM I.5,078 (Pl. 2, figs. 17, 13).

Paratypes. BM IT.497 (Pl. 2, fig. 9) ; BM IT.498 (Pl. 2, figs. 11, 12) ; SMC H.3,778 (Pl. 2, figs. 18, 14) ; SMC H.3,782 (Pl. 2, figs. 15, 16).

Measurements of holotype (in mm.)

Length of pygidium	27·0	Length of axis	5·0
Breadth of pygidium	31·0	Breadth of axis	9·5

Diagnosis. A subspecies distinguished from *S.* (*Scutellum*) *costatum costatum* Pusch by the prominent median rib of pygidium clearly united with axis. Platform less clearly defined from rest of pleural region.

Remarks. The variability of this subspecies renders the selection of a holotype difficult. A specimen near to the norm has been chosen ; this specimen may be distinguished from *Scutellum* (*Scutellum*) *costatum costatum* by the character of the median rib as indicated in the diagnosis. Specimens which lie away from the norm inevitably show additional distinguishing features which affect the vaulting of the dorsal exoskeleton, the character of the median rib, and intercostal furrows. The changes affecting these characters are indicated on page 199.

Scutellum (*Scutellum*) *costatum lummatonensis* subsp. n.

(Pl. 2, figs. 1–8)

Derivation of name. From Lummaton, Torquay, Devon.

Type locality. Lummaton Quarry (SX914665) Torquay, Devon.

Horizon. Middle Devonian. Givetian. Zone of *Maenioceras molarium* (Wolborough Quarry) and of *M. terebratum* (Lummaton Quarry).

Holotype. Pygidium SMC H.2,254 (Pl. 2, fig. 7).

Paratypes. RAMME 66/01 (Pl. 2, figs. 1, 2) ; SMC H.3,801 (Pl. 2, fig. 3) ; RAMME 66/02 (Pl. 2, figs. 4–6) ; SMC H.2,253 (Pl. 2, fig. 8).

Measurements of holotype (in mm.)

Length of pygidium	16·0	Length of axis	3·0
Breadth of pygidium	20·0	Breadth of axis	5·0

DIAGNOSIS. A subspecies of *S.* (*Scutellum*) *costatum* Pusch showing similar range of variation to *S.* (*Scutellum*) *costatum whidbornei* but distinguished by absence of all strong ornamentation.

Scutellum* (*Scutellum*) *delicatum delicatum (Whidborne 1889)

(Pl. 3, figs. 4, 7–9)

1889 *Bronteus delicatus* Whidborne : 29.
1889*a* *Bronteus delicatus* Whidborne ; Whidborne : 33, pl. 3, figs. 14, 14*a*, 15.

TYPE LOCALITY. Wolborough Quarry (SX852705) near Newton Abbot, Devon.

HORIZON. Middle Devonian. Givetian. Zone of *Maenioceras molarium* (Wolborough Quarry) and of *M. terebratum* (Lummaton Quarry).

LECTOTYPE. Cranidium SMC H.4,107 (Pl. 3, figs. 8, 9). Here designated.

SYNTYPES. Pygidium BM I.1,094 ; SMC H.4,106.

FIGURED SPECIMENS. BM I.1,084 (Pl. 3, fig. 4) ; SMC H.3,804 (Pl. 3, fig. 7).

MEASUREMENTS OF LECTOTYPE (in mm.)

Length (*sag.*) of cranidium	28·25	Length (*sag.*) of occipital ring	3·0
Max. breadth of glabella	26·25	Length (*sag.*) of glabella (excluding preoccipital ring)	21·5

DIAGNOSIS. A species of *Scutellum* (*Scutellum*) typically lacking coarse ornamentation. Anterior section of glabella shows pronounced asymmetrical wrinkling of dorsal exoskeleton, weakening and becoming discontinuous posteriorly. Weak elongated nodes appear in same direction along crests of wrinkles ; at first these nodes only represented along flanks of glabella but later also present medianly. Pygidium normally smooth but showing fine, widely spaced pustulation in oblique light. Pygidium characterized by prominent tumid axis weakly divided by longitudinal furrows into three lobes ; median lobe continued posteriorly into prominent undivided median rib larger than all other ribs. Intercostal furrows defining median rib frequently appearing continuous with axial furrows.

DESCRIPTION

In plan the glabella is broader than it is long, and expands rapidly forward to reach a maximum breadth (3 times that at the posterior) near to the anterior margin of the cranidium. The anterior margin of the glabella forms a broad arc reaching to the anterior border at the sagittal line. The glabellar furrows are weakly impressed, the anterior furrows only being recognizable in low, oblique light. 4p is short, transverse and forms a broad but shallow furrow extending from the axial furrow rather more than half the distance towards the sagittal line. It is most deeply impressed at its midpoint, but shallows more rapidly towards the axial furrow than towards the sagittal line. At the axial furrow it lies half the distance (*exsag.*) between the anterior of the glabella and the preoccipital glabellar furrow. 3p forms a shallow traversely elliptical depression lying rather nearer to 2p than 4p and midway between the axial furrow and the sagittal line. 2p is broader and more prominent than the glabellar furrows to the anterior. It is horseshoe-shaped and marginally placed on the glabella so that the anterior and posterior branches run into the axial furrow; that part of the glabella, so isolated, forms a low node. The anterior branch is broader and shallower than the posterior; the latter is most deeply set at the axial furrow. The preoccipital furrow (1p) is transglabellar, deep and broad (*sag.*) and curves gently towards the anterior distally. The median preoccipital glabellar lobe is low and flattened and is inclined from anterior to posterior but scarcely rises above the preoccipital and occipital furrows. The lateral preoccipital glabellar lobes are weakly elevated and recognizable as small nodes lying oblique to the preoccipital furrow. The axial furrows are most deeply impressed posterior to 2p. Between 2p and the posterior of the glabella, the axial furrows are straight and deeply impressed and follow a course almost parallel to the sagittal line. Further to the posterior they shallow, broaden and are deflected weakly outwards at the preoccipital furrow and yet more strongly outwards at the occipital furrow, so that the occipital ring is about one and a half times the breadth (*trans.*) of the glabella posterior. Anterior to 2p the axial furrows shallow and broaden, and diverge from the exsagittal line at 45° and finally unite anteriorly with the anterior border furrow. The anterior border furrow is absent at the median line and only weakly developed at the anterior lateral termination of the glabella. The occipital ring is lens-shaped and prominent, being one and a quarter times longer (*sag.*) than the preoccipital ring. The fixed cheeks are gently inflated; at the posterior they are broad but narrow appreciably towards the anterior. The posterior border furrow is shallow and placed close to the posterior margin of the fixed cheek. The palpebral lobe is small and semicircular in outline; its anterior margin lies opposite the posterior end of the glabella and its posterior margin lies close to the posterior border furrow. At its extremity the palpebral lobe is farther from the sagittal line than any other part of the cranidium. The anterior branch of the facial suture is long and straight. From the anterior end of the palpebral lobe this branch diverges at approximately 10–15° from the exsagittal line and cuts the anterior border close to the axial furrow. The posterior branch of the facial suture is short and swings outwards through a semicircle from the posterior end of the palpebral lobe, to run almost at right angles to the sagittal line. On the line (*exsag.*) of the outer part of the palpebral lobe the suture curves sharply to the posterior to cut the posterior margin three-fifths of the distance from the axial furrow to the genal angle.

Viewed from the front the whole cranidium forms a broad, moderately inflated curve which is broken into 3 sections by the axial furrows into a central glabellar region bounded by the fixed cheeks. The glabella forms a broad, low curve sloping gently away from the crestal point at the sagittal line towards the axial furrows which, in this view, do not appear to be strongly impressed. The palpebral lobe is small and is differentiated from the rest of the fixed cheek only by being slightly more elevated; it rises distally to the height of the crest of the glabella The palpebral furrows are not recognizable. The palpebral lobe and fixed cheek slope gently towards the axial furrow, but dip down rather more steeply at the furrow itself. The combined breadth (*trans.*) of the palpebral lobe and fixed cheek is greater than that of the glabella.

In side view the glabella is low and scarcely rises above the level of the highest parts of the fixed cheeks. The curve of the glabella forms a low flattened arc which rises very slightly from the shallow preoccipital furrow, then slopes gradually to the anterior. Two-thirds of the distance from the posterior of the glabella to the anterior the gradient increases so that the anterior of the glabella forms a more steeply inclined arc. No preglabellar field is apparent. The anterior border is low and insignificant. The preoccipital furrow is shallow and the median lobe of the preoccipital ring is scarcely recognizable ; in this view it is seen only as a gently inclined surface sloping from the occipital furrow to the preoccipital furrow. The occipital ring is prominent rising above the level of the posterior end of the glabella at its crestal point. The occipital furrow is only weakly impressed.

The free cheek is large and subtriangular in shape and is most probably continued postero-laterally into a short, sharp genal spine. The eye is prominent and is strongly curved longitudinally and is elevated to form the highest part of the free cheek, rising to a level equal to half the height of the glabella. The eye surface is convex and marked by many holochroal facets ; it rises steeply from a narrow flattened platform but is separated from it by a weak eye socle. The cheek area is longer than broad and slopes steeply, in an even curve, away from the platform to a broad but shallow lateral border furrow. The lateral border is insignificant and appears as a thin raised area. The posterior border furrow is absent.

In plan the pygidium is semielliptical in outline, being broader than it is long with a length : breadth ratio of 4 : 3. The maximum breadth is attained just anterior to the posterior termination of the axis. The articulating ledge which forms the inner part of the anterior margin is straight and measures approximately one-fifth of the maximum pygidial breadth. This ledge terminates in a small articulating wing, from this point the outer part of the anterior margin curves in an even arc to reach the lateral margin at the point of maximum breadth. The articulating half-ring is broad (*trans.*) and short. The axis is small and subtriangular in outline. At the anterior margin its measurements exceed one-third of the maximum breadth of the pygidium and at the sagittal line it approaches one-fifth of the total pygidial length. The axis is separated from the articulating half-ring by a deep, moderately broad, furrow which is arched forwards medianly and, to a lesser extent abaxially. The axial furrows are narrow and not deeply impressed. The axis is strongly inflated and faintly trilobed. At the anterior border the axis is divided into 3 approximately equal sections by 2 weakly impressed furrows ; these are continued posteriorly broadly parallel to the sagittal line. At the posterior extremity of the axis, the median lobe is of the same breadth as the median rib. The median lobe of the axis is uniformly rounded and the lateral lobes triangular in outline and they become somewhat flattened at the lateral border. The posterior termination of the axis is rounded.

The axial furrows are broad and smooth but not deeply impressed so that they are scarcely marked at the posterior termination of the tail. The central section of the furrows is straight and would, if projected, make an angle of 45° with the sagittal line. Anterior from this central section, the furrows curve outwards rather more gently and posteriorly the axial furrows become continuous with the furrows defining the median rib. No segmentation of the axis has been observed. The pleural region forms a low flattened surface sloping gently away from the low platform bounding the axis. The junction between the platform and the rest of the pleural region is perfectly gradational. The pleural region is divided by narrow deeply impressed intercostal furrows into 7 paired ribs and a single median rib. Paired ribs 1 and 2 are straight and radiate out from the axis. The remaining ribs are gently curved ; from the axis they are directed to the posterior, broadly parallel to the sagittal line, and then sweep posteriorly outwards towards the periphery. All of the intercostal furrows fail to reach the periphery of the tail and, with the exception of those defining the median rib, all furrows weaken towards and fail to reach the axial furrows. Towards the axis the intercostal furrows are deep and have evenly rounded bottoms but, as the furrows broaden towards the periphery, they flatten to reach a maximum of one-quarter of the breadth (*trans.*) of the adjoining ribs. With the exception of the median rib all of the ribs decrease evenly in size from the periphery towards the axis and at the same time the cross-section of the ribs changes from broadly arcuate to convex. At the axis the ribs are a quarter to one-fifth of their width at the periphery. Rib 2 lies between strongly converging intercostal furrows and does not reach so far towards the axis as the adjoining ribs. The median rib is larger than any of the paired ribs ; it is bottle shaped and continuous with the axis.

In side view the axis extends posteriorly for rather less than one-quarter of the total sagittal length of the pygidium and is strongly delimited anteriorly from the articulating half-ring by a deep, evenly rounded furrow. Posteriorly it passes, without a break, into the pleural area. The articulating half-ring is small, at the sagittal line extending anteriorly for a distance equal to the maximum breadth of the articulating furrow. The axis is inflated but somewhat flattened ; it rises steeply from the articulating furrow and then flattens ; the posterior two-fifths of the axis forms a broad arc descending from the flattened area. The platform is flattened to very gently convex, and extends posteriorly for a distance of seven-twelfths of the total post-axial length (*sag.*) and then passes through a gentle curve into a broadly concave slope extending to the posterior margin of the pygidium.

Viewed from the posterior the axis occupies a prominent position and shows a weakly triangular cross-section but is weakly constricted at the midpoints of the slopes away from the sagittal line. The pleural region forms a broad low arc. The platform slopes gently from the axis to its periphery, where it curves in a broad concave slope to the margin of the pygidium. The proximal sections of ribs 1 and 2 are obscured by the slightly more elevated posterior section of the pygidium.

The doublure is broad and very thin and extends more than two-thirds of the distance from the margin of the pygidium to the axis. It is closely applied to the dorsal section of the exoskeleton and ornamented by delicate finely branched terrace lines which run more or less parallel to the border of the pygidium. The spacing of the terrace lines increases towards the axis.

The anterior section of the glabella is ornamented by prominent asymmetrical wrinkles, which represent infoldings of the whole exoskeleton. These are continuous and run more or less parallel to the anterior border of the glabella. Towards the posterior the wrinkling weakens and becomes discontinuous, and at the same time low elongated elevations, which first appear on the lateral flanks of the glabella, become evident along the wrinkle lines. This ornamentation is represented over the whole of the posterior half of the glabella. The posterior parts of the fixed cheeks show a low irregularly spaced granulation but the anterior parts are smooth. The ornamentation of the occipital ring is imperfectly known, but the lateral parts appear to be ornamented by low elongated elevations which are broadly convex to the anterior and lie oblique to the transverse line. The anterior border is ornamented by up to 3 terrace lines.

The pygidium is smooth but in oblique light small irregularly spaced hollow pustules are discernible. It appears that the exoskeleton represented over the pustules is much thinner than that over the rest of the pygidium, so that it becomes transparent and reveals the secondary calcite filling the pustule. All of the furrows on the cranidium and pygidium are smooth.

Scutellum (Scutellum) delicatum tigrinum (Whidborne)

(Pl. 3, figs. 5, 6, 10–12)

1889 *Bronteus tigrinus* Whidborne : 34, pl. 3, fig. 12.
1889*a* *Bronteus delicatus* Whidborne ; Whidborne, pl. 3, fig. 13.
1889*a* *Bronteus granulatus* Goldfuss ; Whidborne, pl. 3, fig. 8.

TYPE LOCALITY. Probably Lummaton Quarry (SX914665) Torquay, Devon.

HORIZON. Middle Devonian. Givetian. Zone of *Maenioceras terebratum.*

LECTOTYPE. BM In.34923 (Pl. 3, fig. 11). Here designated.

SYNTYPE. SMC H.2241. This cranidium is imperfectly preserved and cannot be referred to any species with certainty.

FIGURED SPECIMENS. SMC H.3,785 (Pl. 3, fig. 5) ; BM In.58,998 (Pl. 3, fig. 6) ; BM IT.499 (Pl. 3, fig. 10) ; BM In.34,923 (Pl. 3, fig. 11) ; SMC H.4,106 (Pl. 3, fig. 12).

MEASUREMENTS OF LECTOTYPE (in mm.)

Length (*sag.*) of cranidium	18·0	Length (*sag.*) of occipital ring	2·0
Max. breadth of glabella	19·0	Length (*sag.*) of glabella (excluding preoccipital ring)	12·75

DIAGNOSIS. A subspecies of *Scutellum* (*Scutellum*) *delicatum* (Whidborne) distinguished from type species by coarser ornamentation of dorsal exoskeleton. Ornamentation consists of moderately fine granulation of ribs and axis of pygidium, and moderately pronounced granulation of posterior parts of glabella. Glabella broad, showing maximum length : maximum breadth ratio of 2 : 3.

REMARKS. Whidborne (1889*a*) established the species *Bronteus tigrinus* on the basis of two cranidia only and distinguished it from *Bronteus delicatus* by the broader glabella and by the presence of prominent pits within the axial furrows. Recent collecting has revealed additional material including an almost complete specimen from which it is apparent that the pygidium, like the cranidium, is closely comparable to that of S. (*Scutellum*) *delicatum*. However, it is distinguished quite clearly by a moderate granulation of the dorsal exoskeleton. This granulation is more closely spaced and prominent on the axis than on the ribs. In addition, the axis is less tumid and its threefold longitudinal division is more marked than in S. (*Scutellum*) *delicatum*. The ornamentation of the cephalon is also distinctive; the anterior part of the glabella is characterized by a weak wrinkling giving a broadly continuous series of lines at the anterior margin. These become less prominent and more discontinuous towards the posterior. Small transversely elongated tubercles arise from the lines at the antero-lateral parts of the glabella; these increase in prominence towards the posterior and come to occupy the whole of the posterior section of the glabella. At the same time the tubercles become less clearly elongated and appear as rounded bosses at the glabella posterior. The occipital ring is more finely ornamented than the posterior parts of the glabella, but does show a large prominent mesial tubercle. With the exception of the anterior parts, the fixed cheeks are moderately strongly granulated. The free cheeks appear to be ornamented only by light irregular wrinkling of the dorsal exoskeleton.

Whidborne's two species are thus distinguished primarily by differences in ornamentation; *Bronteus delicatus* being smooth and *Bronteus tigrinus* granulated. This situation is paralleled exactly by the British Middle Devonian forms of *Scutellum costatum*. It appears therefore unwise to attribute more than subspecific significance to the differences in ornamentation and it is proposed to distinguish the granulated form as S. (*Scutellum*) *delicatum tigrinum* and the smooth form as S. (*Scutellum*) *delicatum delicatum*. The possibility of the two forms being varieties of the same species was envisaged by Whidborne (1889*a* : 34).

The separation of the two subspecies on the basis of the ornamentation necessitates the inclusion of one of the specimens (SMC H.4,106) figured by Whidborne (pl. 3, fig. 13) as *Bronteus delicatus* within the subspecies S. (*Scutellum*) *delicatum tigrinum*. The re-allocation of this specimen then allows a further distinction to be drawn; namely that the glabella of the subspecies *tigrinum* shows a maximum breadth : maximum length ratio of 3 : 2, which is appreciably greater than in the subspecies *delicatum*.

A fairly complete specimen of this species (BM IT.499, Pl. 3, fig. 10) shows that 10 uniform segments are present in the thorax. The axis of each segment is broad, but narrower than each pleura, and forms a broad subtriangular arch rising sharply from the flattened pleural areas. Each ring is convex in section and slopes more gently towards the anterior than to the posterior, and is continued anteriorly into a broad (*trans.*) but short (*sag.*) articulating half-ring. The axial furrows are not prominent. The proximal parts of the pleurae show evenly convex median sections which bear narrow flattened anterior and posterior articulating flanges. The distal sections of the pleura are not known.

COMPARISONS. S. (*Scutellum*) *delicatum* is most closely related to S. (*Scutellum*) *costatum* but is distinguished from it by the absence of coarse ornamentation and by the prominent tumid axis and median rib on the pygidium.

Scutellum* (*Scutellum*) *flabelliferum (Goldfuss)

(Pl. 3, figs. 1–3)

1839 *Bronteus flabellifer* Goldfuss: 361, pl. 33, fig. 3*a* (excluding pygidium), 3*c*.

1954 *Scutellum* (*Scutellum*) *flabelliferum* (Goldfuss); Kielan: 28, pl. 4, figs. 6–9, text-figs. 20–23 (includes earlier synonymy of the species).

1955 *Bronteus* (*Bronteus*) cf. *flabellifer* Goldfuss; Maksimova: 43, pl. 1, figs. 2, 3.

1956 *Scutellum* (*Scutellum*) *flabelliferum* (Goldfuss); Richter, R. & E.: 96, pl. 7, figs. 40–42.

REMARKS. Whidborne (1889*a*) and R. & E. Richter (1925) correctly pointed out that because of confusion over specimens figured by Goldfuss (1839, 1843) many specimens from Devon ascribed to this species are properly placed in S. (*Scutellum*) *costatum* Pusch (= *Bronteus granulosus* Goldfuss). *Scutellum flabelliferum* is of rare occurrence and has only been identified from the Chercombe Bridge Quarry where it occurs in a black limestone in association with *Dechenella* (*Dechenella*) *setosa*, Whidborne. The preservation of this material is, in some cases, particularly good; one large pygidium (Pl. 3, fig. 2) shows delicate tooth-like extensions arising from the anterior-lateral border. The median rib of the specimen figured by Whidborne (here re-figured: Pl. 3, fig. 3) is unusual for the species for it has the form more characteristic of *Scutellum costatum*. The presence of this variant within the assemblage tends to confirm that the latter species was derived from *Scutellum flabelliferum*.

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EXPLANATION OF PLATES

All specimens whitened with ammonium chloride before photographing. Specimens prefixed BM., RAMME, SMC and TM. are housed respectively in the British Museum (Natural History), London, the Royal Albert Memorial Museum, Exeter, the Sedgwick Museum, Cambridge, and the Torquay Natural History Museum.

PLATE 1

Scutellum* (*Scutellum*) *pardalios (Whidborne)

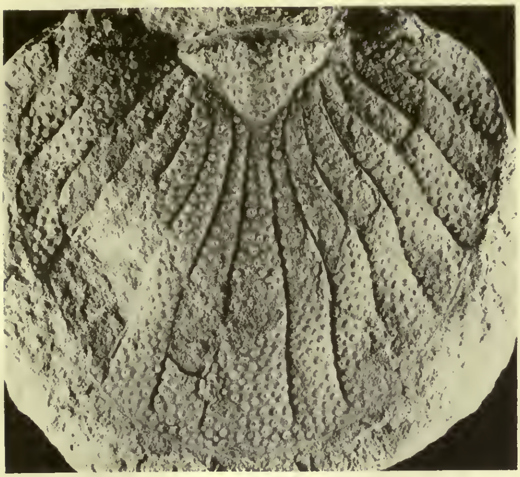
FIGS. 1–3. Pygidium (BM I.100) Lectotype. [Wolborough Quarry]. 1. Plan view, ×1. 2. Posterior view, ×1. 3. Side view, ×1. Figured by Whidborne 1889*a*, pl. 3, fig. 5.

FIGS. 4–5. Cranidium (BM IT.495) Lummaton Quarry. 4. Plan view, ×2. 5. Side view, ×2.

FIG. 6. Cranidium (BM IT.496) Lummaton Quarry. Plan view, ×6. Occipital ring with prominent mesial tubercle.

FIG. 7. Cephalon (SMC H.4,112) Lummaton Quarry. Plan view, ×2·5. Figured by Whidborne 1889*a*, pl. 3, figs. 4, 4*a*.

FIGS. 8–11. Pygidium (RAMME 7149) Wolborough Quarry. 8. Side view, ×1. 9. Plan view, ×1. 10. Posterior view, ×1. 11. Detail of ornamentation, ×3.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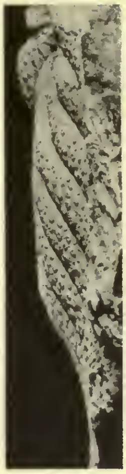
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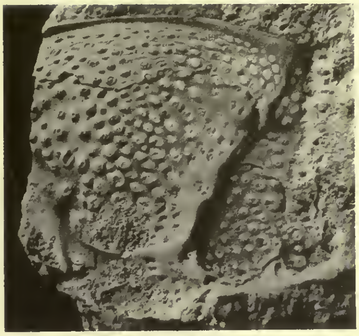
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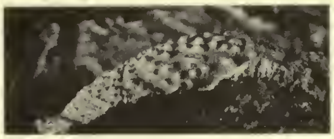
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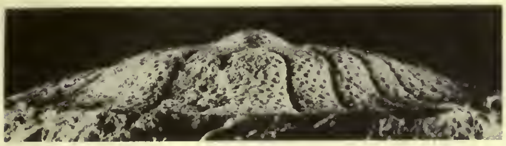
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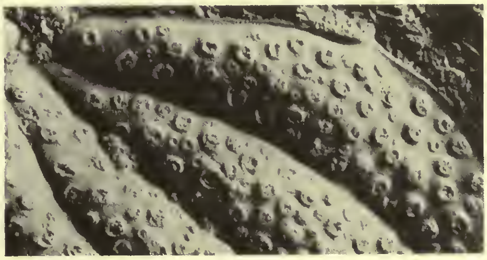
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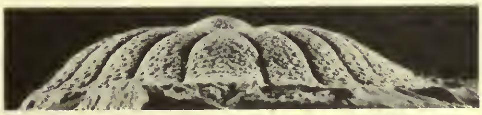
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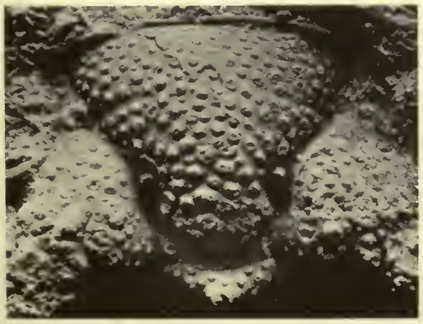
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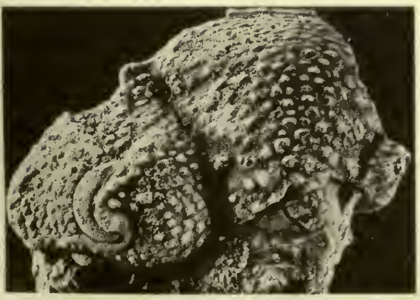
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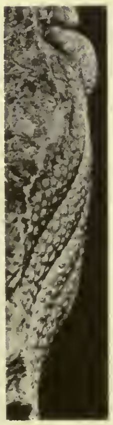
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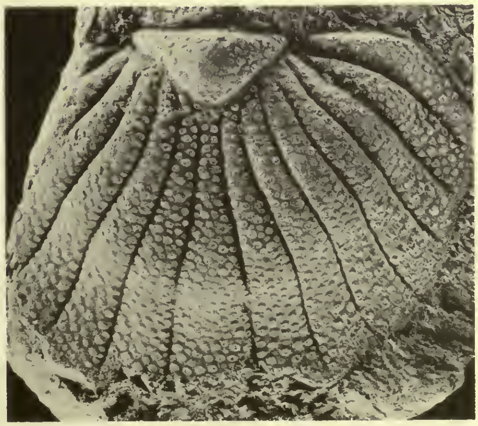
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PLATE 2

Figs. 1, 2. ***Scutellum* (*Scutellum*) *costatum lummatonensis*** subsp. n. Pygidium (RAMME 66/01) [Wolborough Quarry]. 1. Plan view, ×1. 2. Side view, ×1.

Fig. 3. ***Scutellum* (*Scutellum*) *costatum lummatonensis*** subsp. n. Pygidium (SMC H.3,801) Wolborough Quarry. Plan view, ×1·5.

Figs. 4–6. ***Scutellum* (*Scutellum*) *costatum lummatonensis*** subsp. n. Pygidium (RAMME 66/02) [Lummaton Quarry]. Cast. 4. Plan view, ×1. 5. Posterior view, ×1. 6. Side view, ×1.

Fig. 7. ***Scutellum* (*Scutellum*) *costatum lummatonensis*** subsp. n. Pygidium (SMC H·2,254) Holotype. Lummaton Quarry. Plan view, ×1·5.

Fig. 8. ***Scutellum* (*Scutellum*) *costatum lummatonensis*** subsp. n. Pygidium (SMC H.2,253) Lummaton Quarry. Plan view, ×2.

Fig. 9. ***Scutellum* (*Scutellum*) *costatum whidbornei*** subsp. n. Pygidium (BM IT.497) Lummaton Quarry. Plan view, ×1.

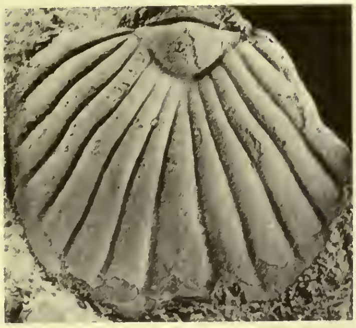
Fig. 10. ***Scutellum* (*Scutellum*) *costatum costatum*** Pusch. Pygidium (TM B.490) Ransleigh Quarry. Plan view, ×1·5.

Figs. 11, 12. ***Scutellum* (*Scutellum*) *costatum whidbornei*** subsp. n. Pygidium (BM IT.498) Lummaton Quarry. 11. Plan view, ×1. 12. Side view, ×1.

Figs. 18, 14. ***Scutellum* (*Scutellum*) *costatum whidbornei*** subsp. n. Pygidium (SMC H.3,778) [Wolborough Quarry]. 18. Side view, ×1. 14. Plan view, ×1.

Figs. 15, 16. ***Scutellum* (*Scutellum*) *costatum whidbornei*** subsp. n. Pygidium (SMC H.3,782) [Wolborough Quarry]. 15. Side view, ×1. 16. Plan view, ×1.

Figs. 17, 13. ***Scutellum* (*Scutellum*) *costatum whidbornei*** subsp. n. Pygidium (BM I.5078). Holotype. Wolborough Quarry. 17. Plan view, ×1·25. 13. Side view, ×1·25.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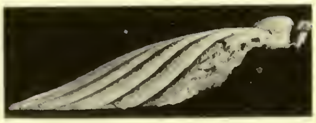
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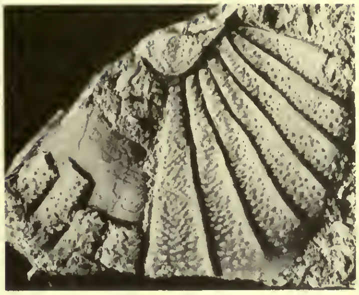
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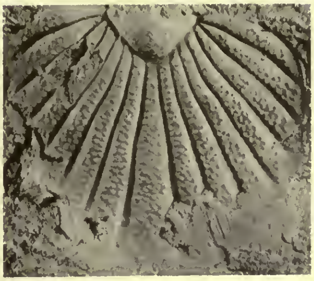
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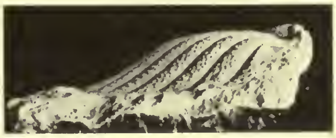
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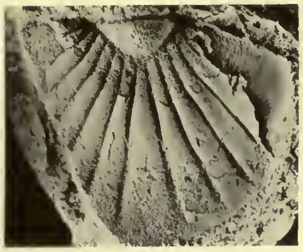
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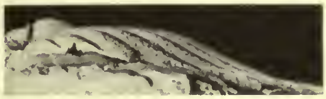
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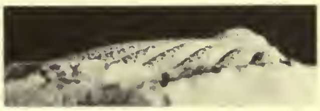
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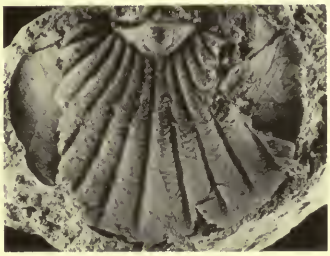
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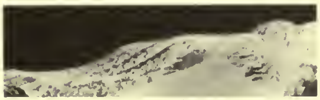
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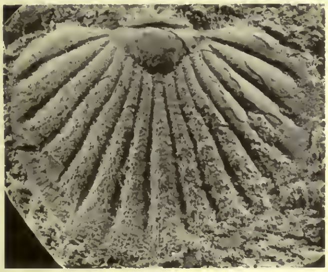
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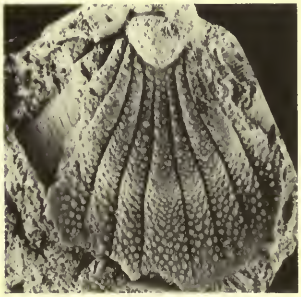
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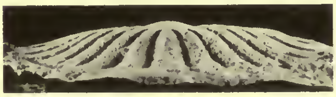
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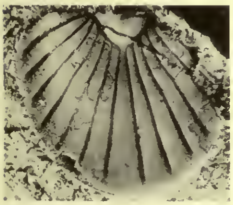
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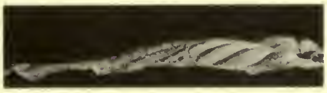
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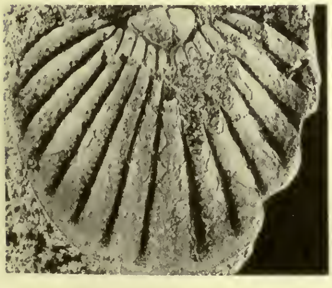
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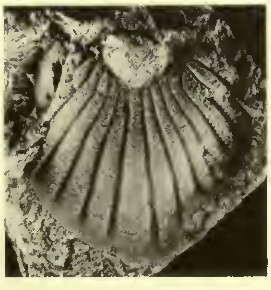
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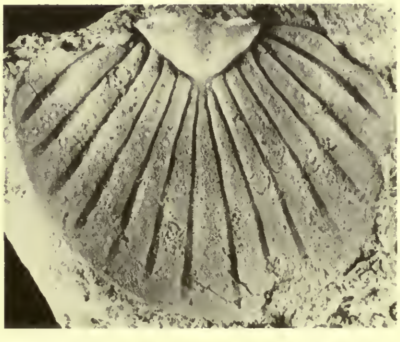
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PLATE 3

FIGS. 1, 2. ***Scutellum* (*Scutellum*) *flabelliferum*** (Goldfuss). Pygidium (RAMME 77/04) Chercombe Bridge Quarry. 1. Plan view, ×1. Cast. 2. Detail showing toothed margin at the anterior lateral margin, ×10. Cast.

FIG. 3. ***Scutellum* (*Scutellum*) *flabelliferum*** (Goldfuss). Pygidium (BM I.5058). Chercombe Bridge Quarry. Plan view, ×3. Figured by Whidborne 1889*a*, pl. 3, fig. 16.

FIG. 4. ***Scutellum* (*Scutellum*) *delicatum delicatum*** (Whidborne). Pygidium (BM I.1084) Lummaton Quarry. Plan view, ×1. Figured by Whidborne 1889*a*, pl. 3, fig. 15.

FIG. 5. ***Scutellum* (*Scutellum*) *delicatum tigrinum*** (Whidborne). Pygidium (SMC H.3,785) Lummaton Quarry, Plan view, ×1·5. Cast.

FIG. 6. ***Scutellum* (*Scutellum*) *delicatum tigrinum*** (Whidborne). Pygidium (BM In.58998) Lummaton Quarry. Plan view, ×1. Figured by Whidborne 1889*a*, pl. 3, fig. 8.

FIG. 7. ***Scutellum* (*Scutellum*) *delicatum delicatum*** (Whidborne). Pygidium (SMC H.3,804) [Lummaton Quarry]. Plan view, ×1.

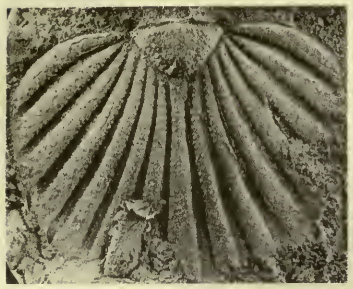
FIGS. 8, 9. ***Scutellum* (*Scutellum*) *delicatum delicatum*** (Whidborne). Cranidium (SMC H.4,107) Lectotype. Wolborough Quarry. 8. Plan view, ×1·5. 9. Side view, × 1·5. Figured by Whidborne 1889*a*, pl. 3, figs. 14, 14*a*.

FIG. 10. ***Scutellum* (*Scutellum*) *delicatum tigrinum*** (Whidborne). Cephalon (BM IT.499) Lummaton Quarry. Plan view, ×2·5.

FIG. 11. ***Scutellum* (*Scutellum*) *delicatum tigrinum*** (Whidborne). Cranidium (BM In.34923) Lectotype. [Lummaton Quarry]. Plan view, ×2·5. Figured by Whidborne 1889,a pl. 3, fig. 12.

FIG. 12. ***Scutellum* (*Scutellum*) *delicatum tigrinum*** (Whidborne). Cranidium (SMC H.4,106) Lummaton Quarry. Plan view, ×4. Figured by Whidborne 1889*a*, pl. 3, fig. 13.

PLATE 3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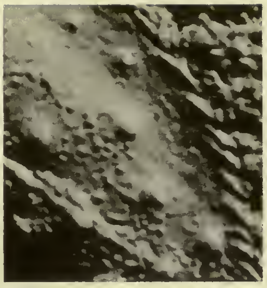
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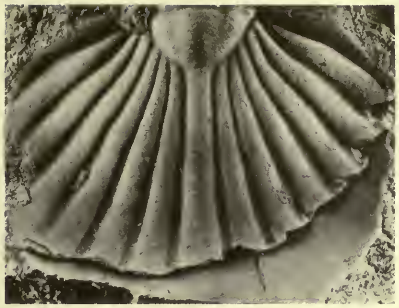
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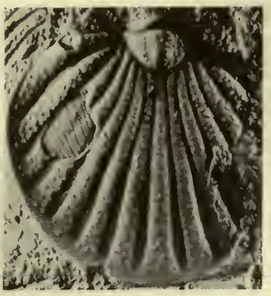
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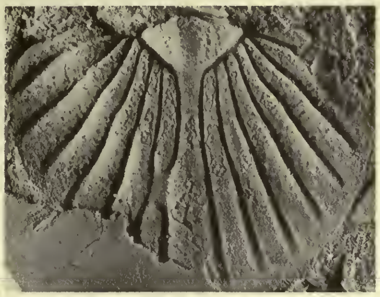
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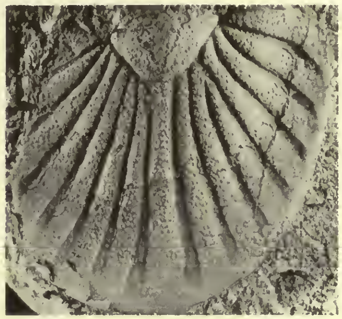
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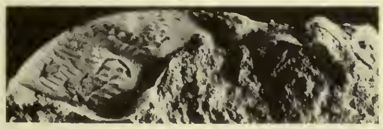
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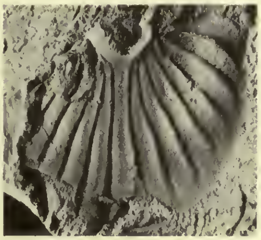
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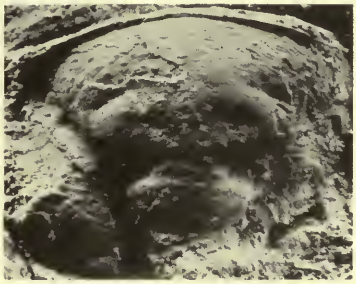
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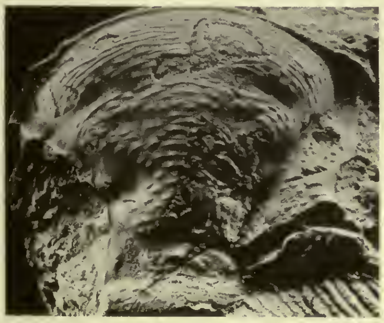
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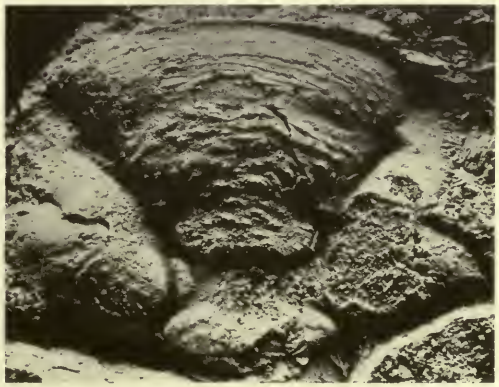
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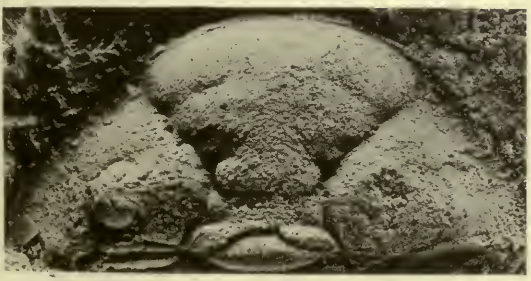
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EXINE STRUCTURE IN SOME FOSSIL AND RECENT SPORES AND POLLEN AS REVEALED BY LIGHT AND ELECTRON MICROSCOPY

J. M. PETTITT

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BY

JOHN MICHAEL PETTITT

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By JOHN MICHAEL PETTITT

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SYNOPSIS

This paper gives descriptions of the wall structure of the spores and pollen grains from a variety of living and fossil plants.

The spores of Palaeozoic heterosporous plants are compared with those of extant homosporous and heterosporous pteridophytes, and Carboniferous pteridosperm and cordaite pollen is compared with that of living cycads and conifers.

It has been found that the structure of the megaspore membrane in some Palaeozoic gymnospermous ovules more closely resembles the spore exine of some free-sporing heterosporous plants than the megaspore membrane of living gymnosperms. Similarly, the exine structure of pteridosperm and cordaite pollen is closer to that of some pteridophyte spores than to the pollen of living gymnosperms. Special attention has been paid to the origin and distribution of the various wall layers, particularly the mesospore and the perispore.

I. INTRODUCTION

The discovery by Ehrlich & Hall (1959) that fine structural detail can be preserved in the exines of Eocene angiosperm pollen has prompted Larson & Lewis (1961) to suggest that the evolutionary development of the pollen wall could be subjected to direct study.

More recently it has been shown that *Classopollis*, a Mesozoic conifer pollen possesses a distinctive wall structure, the complexity of which is unmatched even among living angiosperms (Pettitt & Chaloner 1964).

Afzelius (1956) has investigated the structure of the exine in the spores of living pteridophytes and the pollen of living gymnosperms and angiosperms, and has suggested that certain submicroscopic structures in the exine may be more primitive than others. She suggests that a pollen grain with a thin lamellated layer in the exine may be considered phylogenetically more advanced than one with a thick lamellated layer. Larson & Lewis (1961) discuss this hypothesis and advance the suggestion that fine structural variations in the exine could be related to functional differences. Such a hypothesis would appear to be open to experimental verification, and if it is eventually substantiated any phylogenetic interpretations based on exine structure alone would have to be qualified accordingly.

It has been found that exine fine structure can be preserved in the fossil spores of free-sporing Palaeozoic pteridophytes and in the fossil pollen of Carboniferous seed plants, and that the stratification revealed in ultra-thin sections can be directly compared with the exine structure in the spores of extant pteridophytes and the pollen of living gymnosperms. The following is an attempt to synthesize the information so far obtained.

II. METHODS OF INVESTIGATION

The fossil material was released from the enclosing sediment with cold commercial (40%) hydrofluoric acid. Where necessary dilute nitric acid was used to clean and soften the spores and pollen prior to dehydration and embedding. Details of the fixation, embedding and histological procedures used in this investigation are given in Pettitt (1966).

Ultra-thin sections were cut either on a Huxley-pattern or a Reichert ultramicrotome using glass knives and mounted on copper grids with or without carbon reinforcement for observation with a Siemens' Elmiskop 1a or an A.E.I. EM6B electron microscope operating at 60 kV. Some use has been made of section stains and where they have been employed the fact is recorded in the figure legends.

Thicker sections (about 0·2 μ) of methacrylate and epoxy resin embedded specimens examined under phase and anoptral contrast illumination have been used fairly extensively in the investigation of the thicker exines.

The terminology adopted for the exine subdivisions revealed in the spore and pollen walls follows that proposed by Faegri (1956). Although this system of nomenclature was applied to explain the subdivisions detectable in the exine of angiosperm pollen following alcoholic basic fuchsin staining, Larson (1964) by using electron stains has shown that it is probably also applicable to the spores and pollen of non-angiospermous plants.

Acknowledgments

I am indebted to Mr. Clive Jermy of the Department of Botany, British Museum (Natural History) for supplying a great deal of the modern pteridophyte material, to Professor R. W. Baxter of the University of Kansas for allowing me to work on the Lawrence Shale fossils, to Dr. T. N. Taylor of the University of Illinois for sending me seed petifications and to Dr. W. G. Chaloner for providing the samples of Scottish coals. I should like to express my very sincere thanks to Professor

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III. DESCRIPTIONS

SPORES OF LIVING AND FOSSIL HETEROSPOROUS PTERIDOPHYTES

Spores of *Archaeopteris* cf. *jacksoni* Dawson

The occurrence of heterospory in this Devonian species has already been described (Pettitt 1965) and a full description of the morphology of the spores is given in that publication.

Megaspores. The subdivision of the megaspore exine into an outer granular layer and an inner apparently homogeneous layer has been detected with the optical microscope (Pettitt 1965). At that time it was recorded that some, but not all, of the megaspores possessed a conspicuous inner body or mesosporium. It was not possible, however, to see how the inner body was formed nor to determine precisely how it was related structurally to the remainder of the spore wall.

Ultra-thin sections of the megaspores from a sporangium of *A.* cf. *jacksoni* examined in the electron microscope support the interpretation based on the observations with the optical microscope. The thin, inner layer (endexine) which appears homogeneous in sections under the light microscope is seen to have a lamellated structure, whilst the outer optically "granular" layer (ektexine) is composed of three-dimensional, anastomosing sporopollenin units giving the layer a spongy appearance (Pl. 2, figs. 1, 2 ; Pl. 3, fig. 3). The outer spongy layer accounts for the greater part of the thickness of the wall.

The subdivision of the inner lamellated layer or endexine into a series of concentric lamellae is evident in all the micrographs. In some sections there is partial or complete separation of this layer into an inner and an outer zone (Pl. 3, fig. 3). The separation would appear to be along one of the periods between the lamellae and the fact that it does not occur in all the megaspores, together with the observation that the actual site of the separation within the layer varies in the different spores would suggest that it is not a regular feature of ontogeny.

From the evidence it seems reasonably certain that the separation of the endexine in these megaspores is responsible for the presence of the inner body or so-called mesosporium that can be observed in entire spores examined by transmitted light (Pettitt 1965).

In the earlier publication I provisionally assigned the megaspores of *A.* cf. *jacksoni* to the megaspore genus *Biharisporites* Potonié (1956) using the presence of a mesospore in some of the specimens as one of the features indicating a close correspondence with the spores of that genus. However, the discovery that the mesospore of these fossils is probably formed by the artificial separation of the inner layer of the exine into two immediately calls to question the validity of the feature as a taxonomic character.

The structure and formation of mesospore-like bodies in the spores of other fossil plants and in the spores of living pteridophytes is discussed later.

Electron micrographs of sections through *Archaeopteris* megaspores that are situated at the outside of the sporangial mass show an unusual feature. On the surface of these spores dense aggregations of droplets occur in close association with the underlying spongy layer of the exine. The droplets vary in size, and consist of an outer stratum of homogeneous sporopollenin which becomes granular towards the centre of the body. The droplets have a hollow central lumen which is traversed by irregular wefts or threads of material with a coarsely granular fine structure (Pl. 2, fig. 1). There is no evidence of structural connexion between any of these bodies and the outer part of the exine, and they cannot be regarded as part of the wall ornamentation in the strict sense. Recent observations on the formation of sporopollenin droplets in the degenerating tapetal cells of gymnosperm pollen sacs (Pettitt 1966) leaves little doubt that the droplets in the *Archaeopteris* sporangia have a similar origin. Rowley (1963) has called somewhat similar droplets Ubisch bodies in the pollen sacs of angiosperms, but as Ubisch bodies seem to have a functional role in pollen wall formation in these plants it would be unwise to apply the name to the droplets in the *Archaeopteris* megasporangia. They are perhaps more comparable to the objects which Ueno (1959, 1960) has described as the perine in the pollen of some gymnosperms. This point is more fully discussed in a later section.

Finally, it is evident that such deposits on the outer surface of the spore exine could easily be mistaken for sculptural elements in an uncritical examination.

Microspores. The microspore exine of *Archaeopteris* cf. *jacksoni* is divided into two distinct layers which, in their ultrastructure, closely resemble the layers of the megaspore exine. The inner layer (endexine), which lines the lumen of the spore, is lamellated, whilst the outer layer (ektexine) is composed of ramifying units of sporopollenin giving the layer a spongy appearance (Pl. 3, fig. 1). In addition to the fine structure and stratification of the exine, thin sections through the spore wall show some other features that warrant description.

The electron micrograph shown on Pl. 3, fig. 2 is of a section which passes through one of the triradiate commissures. The section clearly shows that the lamellated endexine passes upwards through the commissure and forms a lining to the aperture. On the surface of the spore the endexine overlaps on to the outer layer of the exine and gradually thins out. It seems probable that the structures just described are lips, although lips surrounding the triradiate laesurae of these microspores were not detected with transmitted light (Pettitt 1965).

The exine ornamentation of the microspores of *A.* cf. *jacksoni* has been described as being composed of minute conical elements about 1–1·5 μ in height, and 1 μ or less wide at the base (Pettitt 1965), and on the basis of this they were provisionally assigned to the genus *Cyclogranisporites* Potonié & Kremp 1954. The electron micrographs show how the conical elements are constructed from the sporopollenin units forming the outer exine layer (Pl. 3, fig. 1).

The spores of *Selaginella* and *Isoetes*

Megaspores of Selaginella. The electron micrographs of the acetolyzed megaspore of *Selaginella selaginoides* published by Afzelius, Erdtman & Sjöstrand (1954) show that the wall is composed of a " three-dimensional network of rounded bars ". An almost identical fine structure has recently been observed in *Selaginella myosurus* and *Selaginella kraussiana* by Stainier (1965), and from the observations made during the present investigation it would seem that the outer layer of the megaspore exine in a number of *Selaginella* species is of this composition. The following description is, however, based mainly on the megaspores of *Selaginella pulcherrima* Liebm.

Sections of the megaspore wall examined by phase contrast illumination show that there are structural variations within the outer exine layer. These are evident as concentric zones in the ektexine that appear to result from variations in the amount of interstitial space between the elements composing this layer of the wall. Electron micrographs show that at the outer edge of this outer layer the sporopollenin units become discontinuous and the wall texture is more open or porous in appearance. Towards the inner limit of the layer the sporopollenin elements gradually become reduced in thickness and less widely spaced and the boundary is seen as a zone of more compact structure (Pl. 4, figs. 1, 2). Martens (1960) and Stainier (1965) have detected obvious zoning in the megaspore exine of *S. myosurus* and they find that the sporopollenin units in certain parts of the exospore have a definite orientation which would seem to be unique to this species.

The acetolyzed megaspore wall of *Selaginella* consists mainly of a very thick, spongy outer layer or ektexine. On the inside of this, however, is a much thinner layer, the endexine, which accounts for not more than one-twentieth of the total thickness of the exine. Although the endexine has not been adequately photographed in the electron microscope it can be clearly seen in thin sections that were examined and photographed by anoptral contrast illumination (Pl. 5, fig. 1). In these sections the endexine appears to be faintly lamellated, and the junction between it and the ektexine is very distinct.

Fitting (1900) published a very detailed account of megaspore development and structure in *Isoetes* and *Selaginella*. As his observations are of significance to the present study the more relevant of them should perhaps be briefly reviewed.

Fitting recognizes three or sometimes four layers in the megaspore wall of *Selaginella*. The outer layer in some species is a thick silicified " perispore ", but this is not always present. Underlying the perispore is the exospore which is often differentiated into two layers. Within the exospore is the mesospore, a very thin, yellowish membrane that is easily separated from the overlying layer. The innermost layer recognized by Fitting is a cellulosic endospore.

Fitting followed the development of the sporoderm in *Selaginella* megaspores and sets out a very precise series of events. He found that the exospore is the first formed layer and that this increases in thickness to between 0·5–1·2 μ (depending on the species) before the mesospore is formed. According to Fitting the mesospore is formed as a new layer and does not arise as a result of splitting in the exospore. The fact that from its inception there is sometimes a gap between the mesospore and the exospore is advanced as evidence for formation *de novo*. Following its formation the mesospore rapidly increases in thickness.

In this connexion it is worth noting that Fitting observed two rather relevant differences in the megaspores of *Selaginella galeotii* on the one hand and *Selaginella spinulosa* and *Selaginella helvetica* on the other. In the first species a distinct margin between the exospore and the mesospore is not evident, whilst in *S. spinulosa* and *S. helvetica* there is a division in the middle of the exospore extending from the proximal to the distal surface which divides the layer into two membranes of equal thickness.

Fitting noticed that as the megaspores increase in size the exospore and the mesospore become separated from each other and from the spore protoplast. The layers remain firmly attached at the spore apex and the separation can be detected first in the distal region of the spores and later in the equatorial region. There is apparently some variation in the stage at which this separation occurs and in the extent to which it finally develops. An extreme example would seem to be the megaspores of *S. spinulosa* where the two layers remain firmly attached at all times. In the megaspores of some species bars or trabeculae, which have the same composition as the spore wall, were seen to link the exospore and the mesospore together. These structures are rather short-lived, and with the increase in size of the spores they become thinner and finally rupture. Fitting regards the presence of the trabeculae in *Selaginella* as indicative of close connexion between the exospore and the mesospore in young megaspores, and he believes that they originate as a result of polymerization or coalescence of the two membranes at their points of contact. The trabeculae are formed at the sites of contact as the membranes draw apart during spore growth and the space between them increases. The space between the two wall layers and between the mesospore and the spore protoplast is filled with an interstitial substance (more evident in older spores) which Fitting found to give a pectin reaction and also to stain with Congo red and Analine blue.

The interstitial substance gradually disappears as the megaspores mature and the mesospore expands until it makes contact with the exospore. Both layers then grow in circumference with the result that in the mature megaspores the thick mesospore present in the early stages of development is present as a thin membrane closely associated with the exospore.

Somewhat later the cellulosic endospore is formed and the protoplast increases in mass and fills the spore lumen. About this time the perispore is formed from the lamellae of the special mother cell wall.

Of the two papers published by Lyon (1901, 1905) describing exine formation in *Selaginella* the latter is the most pertinent to the present account. In this, Lyon questions some of the conclusions reached by Fitting (1900) and revalues the earlier work of her own. Lyon detected only two megaspore wall layers in the material she investigated; the exospore, which is formed first, and the endospore, which is lamellated. Some confusion arises here because the layer that Lyon (1905) calls the endospore is the layer which Fitting (1900) calls the mesospore. Lyon does not find a mesospore *sensu* Fitting in her material.

Lyon's investigations lead her to conclude that the exospore and the endospore (mesospore of Fitting) are sometimes formed simultaneously, and that the space which occurs between these two layers is an artifact caused by shrinkage. Lyon's evidence for this suggestion is based on the observation that in some megaspores the membranes do not separate. Lyon also finds that in young megaspores there is a tendency for the exospore to split into an outer and an inner layer and that the inner part of the exospore, to which the endospore is attached, could be interpreted as a separate wall layer.

Campbell (1902) suggests that the cavity between the wall layers of the megaspores originates as a result of the exospore enlarging more rapidly than the mesospore. According to this author the mesospore closely resembles the exospore in appearance and could arise by the separation of an inner layer from the exospore.

More recently, Stainier (1965) has recognized four wall layers in the megaspore of *S. myosurus*, which correspond to the four detected by Fitting (1900), and three in *S. kraussiana*. This author finds that the mesospore is separated from the exospore in both these species and concludes that the separation in *S. myosurus* is a natural phenomenon which occurs during spore growth but in *S. kraussiana* it is probably a fixation artifact.

The descriptions given by Fitting (1900), Lyon (1905), Campbell (1902) and Stainier (1965) show that whilst there is some measure of agreement in the naming of the various exine subdivisions that these authors detected in the megaspores of *Selaginella* it is far from being absolute. It is difficult, for example, to accept that the layer which Fitting describes and illustrates as the mesospore in young *Selaginella* megaspores is identical with the layer to which Campbell gives the same name. It is apparent that the term mesospore is being applied to very different structures.

The importance of an inner body or mesospore as a microscopical character in the recognition of a number of fossil microspore and megaspore genera has already been mentioned. There is some difference of opinion as to whether this structure is an artifact (see Kremp 1965) and the conflicting evidence from living material hardly helps to resolve these differences. It is of some interest, therefore, to try to establish the true nature of the mesospore.

Sections of *S. pulcherrima* megaspores containing mesospores of the type illustrated by Fitting (1900, pl. 6, fig. 23) in his immature megaspores were subjected to a variety of histochemical tests. It should be pointed out that possibly only one or two of the four megaspores in any one sporangium contained mesospores of this type. Judging solely from their external appearance all the spores at first seemed to be perfectly normal. However, sections showed that normal protoplasmic contents, whilst present in some of the spores, are completely lacking in the spores that contain a mesospore. This observation completely contradicts those of Fitting (1900) and Lyon (1905).

Structurally the central part of the mesospore appears fibrous under the light microscope at high magnifications and the fibrosity gives way to a more granular structure towards the periphery of the body. In the centre is a hollow cavity (Pl. 5, fig. 4). Trabeculae linking the mesospore with the ektexine (exospore of

Fitting) are sometimes present. The endexine could not be detected in megaspores that contained a mesospore.

Sections stained with Sudan black B show that the entire mesospore and the ektexine are strongly sudanophilic (Pl. 1, fig. 5). Following treatment by the periodic acid/Schiff (PA/S) procedure the central, fibrous zone of the mesospore gives a vivid red colour, but there is no reaction from the outer granular zone, nor from the ektexine (Pl. 1, fig. 3). This staining pattern is repeated in sections stained with ruthenium red. It is, however, reversed in sections stained with Nile blue sulphate. The inner fibrous zone stains faintly, if at all, whilst the outer granular zone of the mesospore and the ektexine stain a strong blue colour (Pl. 1, fig. 4). From these tests it can be reasonably concluded that the inner fibrous zone of the mesospore gives positive indications of the presence of lipids and carbohydrates.

Further characterization of the nature of the body was obtained after treating sections with mercuric bromophenol blue, developed as a protein indicator by Mazia, Brewer & Alfert (see Pearse 1961). It was found that the ektexine and the outer granular layer of the mesospore remains unaffected by this test, but that the inner fibrous zone is coloured faintly blue-green (Pl. 5, fig. 3).[1]

As a measure of control, sections of megaspores that did not contain a mesospore were subjected to the same histochemical procedures. Following acetylated Sudan black B staining the spore protoplast colours strongly and three sudanophilic wall layers are recognizable; the ektexine, the endexine which is frequently detached from the ektexine except at the spore apex and a thin membrane closely associated with the spore protoplast. The identity of this last layer is only clearly recognizable where the protoplast has become separated from the outer wall layer (Pl. 1, fig. 6). At the apex of the megaspore, where cellular differentiation has occurred, the membrane is seen to have anticlinal walls which closely match the position of the cell walls of the underlying gametophyte tissue. So far, this layer has been detected only in the megaspores of *S. pulcherrima* and in this respect these spores would seem to be unique.

Between the membrane just described and the endexine is an optically structureless layer that does not colour with the Sudan stain but which stains intensely with ruthenium red. This layer, which is not always detectable can, by analogy with pollen wall terminology, be called the intine and is presumably that which Fitting (1900) and Stainier (1965) call the endospore.

The ektexine is coloured bright blue after Nile blue sulphate staining, whilst a subtending layer, which from its position would appear to be the intine, stains a strong purple colour. The blue coloration of the ektexine following the Nile blue sulphate method indicates that this layer contains a high proportion of acidic lipids, whilst the purple colour of the inner layer following the same test would suggest that this contains predominantly neutral lipids. The discovery that the inner layer is composed of pectic substances that are stained with ruthenium red and neutral lipids is somewhat surprising, and perhaps the analogy with the pollen intine extends only to the location of the layer and not to its composition. Stainier (1965) has shown that the endospore of *S. myosurus* is cellulosic.

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[1] It has proved impossible to obtain a colour-faithful photomicrograph of this test and, consequently, it has not been included in Pl. 1.

Following section treatment by the PA/S test the intine and the thin sudanophilic membrane that surrounds the protoplast give a strong red colour characteristic of a positive Schiff reaction. The protoplasmic contents of the megaspore stain faintly (Pl. 1, figs. 1, 2).

Preparations treated with mercuric bromophenol blue reveal the presence of proteins in the megaspore protoplast which is coloured blue-green after this procedure (Pl. 5, fig. 2, see footnote on p. 230). No reaction is seen from the megaspore wall layers.

The evidence from these histochemical methods strongly suggests that the mesospore, *sensu* Fitting, in these spores is not composed of sporopollenin. Although the presence of lipid in the ektexine, the endexine and the mesospore is clearly demonstrated by Sudan black B staining, the mesospore, or more correctly the central zone of it, also gives positive reactions for carbohydrates, pectin and proteins. Carbohydrates, pectin and proteins were not detected in the ektexine or endexine, but carbohydrates and proteins do occur in the normal megaspore protoplast. The only conclusion that can be drawn from these results is that the mesospore is chemically more closely allied to the spore protoplast than to the exine.

The occurrence of the mesospores in megaspores without a recognizable protoplast together with the histochemical evidence suggests that the inner fibrous zone of the mesospore represents an abortive protoplast that has undergone serious deformation at some stage during its development. The outer granular zone of the body behaves chemically like the exine material and the presence of this layer may be correlated with the apparent absence of an endexine in these spores. Presumably the resistance of the mesospore to acetolysis could be explained by the presence of the lipid and protein.

An entirely different interpretation can, however, be placed on the structure which Fitting (1900) and Stainier (1965) designate the mesospore in mature spores of *Selaginella*. In mature megaspores of *S. pulcherrima* and *Selaginella padangensis* Hieron. with normally developed protoplasts the endexine is frequently found detached from the ektexine. This is clearly seen in sections of acetolyzed megaspores where the endexine is present as a distinct inner layer, separated from the ektexine by a narrow cavity, and enclosing a central lumen. These preparations also show that the ektexine is frequently split, particularly in the apical region, a phenomenon to which Lyon (1905) draws attention. Sections through the apical region of the megaspores show that the endexine is attached to the ektexine in the region of the triradiate sutures in precisely the way that Fitting (1900) describes for his " exospore " and " mesospore ". Not infrequently it can be seen attached over a much greater part of its circumference. The frequent apical attachment of the endexine to the ektexine is explained by serial sections cut tangentially through the proximal region of the megaspores. These show that the endexine passes up into the triradiate commissures of the spore in exactly the same way as in the microspores of *Archaeopteris* (Pl. 5, fig. 5).

It would appear that the mesospore recognizable in the normal, mature and presumably viable megaspores of *Selaginella* is in no way identical to the structure given that name by Fitting (1900) in the spores which he believed to be immature but which are probably abortive. In normal, mature *Selaginella* megaspores the mesospore is formed by the endexine separating from the ektexine around most of its circumference as suggested by Stainier (1965) for *S. kraussiana*, but remaining attached to the outer layer at the triradiate laesurae. Fossil megaspores containing precisely this type of structure are described in the previous section. In contrast, the central body or so-called " mesospore " of abortive *Selaginella* megaspores is probably a protoplasmic remnant which has undergone considerable structural deformation. Whether or not this structure which will survive acetolysis and oxidative maceration would also survive fossilization is questionable.

Microspores of Selaginella. Ultra-thin sections of microspores of *S. pulcherrima* show that the entire thickness of the exine is composed of sporopollenin that appears homogeneous or faintly fibrous in the electron microscope (Pl. 5, fig. 6). There is no evidence of an inner lamellated endexine. The fine structure of the microspore wall of this species is, therefore, very different from that of the megaspore.

Surrounding the entire microspore and interrupted only at the triradiate commissures is a thin, electron-opaque layer which has a somewhat granular ultrastructure. In the megaspores of the same species a well-demarcated, phase-white, granular layer can be seen on the outside of the exine when sections are examined by anoptral contrast illumination (Pl. 5, fig. 1). Fitting (1900) describes a granular silicified layer on the outer surface of the *Selaginella* megaspores to which he gives the name " perispore " and it is reasonable to assume that the granular electron-dense and phase-white layers in *S. pulcherrima* could bear the same interpretation. The optical appearance of the layer suggests that it is an inorganic substance (probably silica) that has been deposited on the outer surface of the exine. The question of whether this should rightly be called a " perispore " in the sense that the term has now been defined is discussed later.

Following histochemical tests with Sudan black B, Nile blue sulphate, PA/S and mercuric bromophenol blue the microspores of *Selaginella* behave in much the same way as those megaspores lacking a mesospore. The exine is seen to be sudanophilic and colours blue after treatment with Nile blue sulphate, but gives no reaction after the PA/S test. The siliceous " perispore ", however, of both the microspore and megaspore stains vividly with celestin blue (Pl. 1, fig. 2). The spore protoplast is stained faintly red after PA/S treatment, and a strong blue-green colour after section treatment with mercuric bromophenol blue. The microspore exine is not coloured by the protein test.

Megaspores of Isoetes. In his account of the structure of the megaspore of *Isoetes* Fitting (1900) divides the wall into four layers which are, from the outside inwards, a strongly silicified perispore, an exospore (which is often split into three sub-layers), a thin mesospore and a cellulosic endospore. The extent to which the perispore is developed varies somewhat in different species and it forms the ornament in those megaspores which are ornamented. The ornamentation is repeated in the underlying exospore. There is, therefore, a close association between the perispore and the exospore in *Isoetes* and some interbedding is not uncommon. Fitting's study shows that the perispore is laid down only when the megaspores are mature.

In most species of *Isoetes* Fitting finds that the exospore is clearly divided into three subdivisions or lamellae. This feature is particularly clear in those species which have a thick exospore, and apparently transitions exist within the genus from spores in which exospore stratification is clearly recognizable to those in which none can be seen.

Fitting describes the exospore of *Isoetes* as being composed of small, dark brown " crystalline " rods which are arranged parallel to the surface of the spore. The rods are more closely packed in the middle zone of the layer than in the outer or the inner zones.

The mesospore is described as a thin layer that in both young and mature spores is always somewhat separated from the exospore and which has the same chemical composition as the latter.

The cellulosic endospore is intimately connected with the mesospore which, according to Fitting, exhibits some stratification following treatment with cuprammonium. Between the endospore and the spore protoplast is a thin " pellicle " that gives a positive reaction for pectin.

In *Isoetes*, as in *Selaginella*, the exospore is the first wall layer to be formed and the mesospore, which Fitting believes to arise *de novo* as in *Selaginella*, is formed somewhat later. The formative events closely parallel those of *Selaginella* and as the megaspore increases in size the mesospore separates from the exospore, remaining attached at the proximal pole. In some species, mesospore separation does not take place at all or only to a very limited extent. Endospore deposition occurs when the megaspores have almost attained their full size.

One further point is worth recording. Fitting (following Tschistiakoff) recommends that the term " epispore " should be applied to the membrane or membranes formed from the " Epiplasma " (the tapetum ?) and the term perispore to that of those formed from the special mother cell wall. Following these definitions, the outer silicified layer of *Isoetes* megaspore walls, which Fitting describes as originating from the inner layers of the special wall, would be a perispore.

Ultra-thin sections for electron microscopy which show exine structure in *Isoetes* megaspores have not so far been obtained. Thin sections for examination by optical microscopy are much easier to cut and form the basis of the following description.

Pl. 5, figs. 7, 8 are anoptral contrast photographs of thin sections of megaspores of *Isoetes humilior* F. Müll. ex A. Braun that were soaked in hydrofluoric acid to remove the siliceous material from the exine and acetolyzed prior to embedding in epoxy resin. The resolution attainable by this method of examination is sufficient to confirm Fitting's (1900) observation that the exospore (ektexine) is composed of small " crystalline " rods arranged parallel to the surface of the spore. Histochemical tests on megaspores not subjected to hydrofluoric acid treatment show, however, that the exine elements or rods are composed of sporopollenin.

Although the arrangement of the sporopollenin elements forming the ektexine in the megaspores of this genus somewhat resembles that seen in *Selaginella*, there are some marked differences. Comparison of the micrographs of *Selaginella* (Pl. 4, figs. 1, 2 ; Pl. 5, fig. 1) with those of *Isoetes* show that in the latter the ramifying rodlets of the ektexine are thinner and much less densely packed than in *Selaginella*, the general effect being that the *Isoetes* exine appears to have a more " open " texture. A second difference is that an inner lamellated endexine was not detected in the megaspores of *Isoetes*.

In a number of megaspores of *Isoetes* that were examined as both sections and entire objects the inner part of the ektexine is seen to be separated from the remainder (Pl. 5, fig. 8 ; Pl. 6, fig. 1) as described by Fitting. The separation would seem to be quite unrelated to the age of the spores, and evidently occurs along a plane of weakness in the exine. It is never complete around the full circumference of the megaspore and attachment is always maintained at some point, usually the proximal pole.

Microspores of Isoetes. Electron micrographs of *Isoetes echinospora* Dur. microspores show that the exine consists of two layers, the outer is lamellated and the inner homogeneous (Pl. 6, figs. 2, 3). The lamellae of the outer layer appear to anastomose in some sections and the layer then appears structurally not unlike the ektexine of the megaspores. The arrangement of these subdivisions is particularly interesting because the microspores of this genus are the only spores so far examined where the outer layer of the exine is lamellated. Nilsson & Praglowski (1963) however, call this layer the perine and do not, therefore, regard it as part of the exine *sensu stricto*. This interpretation, together with the question of just what does and what does not constitute a perine, is discussed later.

The electron micrographs and phase contrast pictures show that in *Isoetes*, although there are some structural differences between the exine of the microspores and that of the megaspores, they are not so marked as they are in *Selaginella*.

The phase contrast pictures of sections of acetolyzed microspores from a single sporangium of *Isoetes echinospora* (Pl. 7, figs. 1–8) show that the inner layer of the exine is invariably detached from the outer, but the occasional spore exhibiting complete unity between these two layers, presumably the normal condition (Pl. 7, fig. 1), serves to suggest that the separation is either an unusual feature of development or an artifact induced by fixation. Variations in the extent to which the layers have separated are shown. In some of the microspores the inner layer is attached only at the proximal pole (Pl. 7, figs. 4, 5) and in others only at the distal pole (Pl. 7, figs. 2, 3). One example shows a condition where the inner membrane is attached laterally and is completely free at both the proximal and distal poles (Pl. 7, fig. 8) and others where the inner membrane is completely free from the outer around its entire circumference (Pl. 7, figs. 6, 7). Thus, within a single microsporangium of *Isoetes*, spores can be found that could be classified when dispersed as either cavate or not so, if the current definition for this structural condition was applied to them (see Dettman 1963, Kremp 1965).

Somewhat similar variations in the arrangement of the wall layers occur in the microspores of *Marsilea* that are described below.

The wall structure of *Laevigatisporites* cf. *glabratus*

Megaspores identified as *Laevigatisporites glabratus* (Zerndt) Potonié & Kremp 1954 were recovered from the Lawrence Shale (Virgillian) of Lone Star Lake, Kansas by digesting the sediment in cold hydrofluoric acid. Megaspores of the *Laevigatisporites* type have been recorded from a number of Carboniferous Sigillarian fructifications (see Chaloner 1953).

Electron micrographs (Pl. 7, fig. 10) and phase contrast photographs (Pl. 6, fig. 5) show that the entire thickness of the exine is composed of the familiar ramifying units of sporopollenin. The presence of an inner wall layer (endexine) bordering the spore lumen was not detected, but Schopf (1941) has found two wall layers in the microspores of *Mazocarpon oedipternum* (a Sigillarian cone with *L. glabratus* megaspores).

The spores of *Marsilea* and *Regnellidium*

Megaspores of Marsilea. Feller (1953) and Boterberg (1956) have both described the structure and development of the megaspores and microspores in *Marsilea*—Feller in *Marsilea hirsuta* and Boterberg in *Marsilea diffusa*. Both authors compare their observations with those published by Meunier (1888) on the structure of the sporocarp and spores of *Pilularia globulifera* and Boterberg compares his with those of Bonnet (1955).

Although Feller's and Boterberg's respective accounts of spore ontogeny in *Marsilea* differ in some relatively minor details they both conclude that the megaspore in the species they have investigated is composed of an inner endospore and an outer exospore. Three outer, rather unique gelatinous layers surround the exospore, but these are not considered in this account.

According to these two authors the endospore is the first megaspore wall layer to develop and when fully differentiated in the mature megaspore it consists of two layers. From the evidence presented by these authors the inner endospore probably corresponds to the intine of an angiosperm pollen wall; the outer layer is sudanophilic. In young megaspores the endospore is often found detached from the remainder of the wall.

The structure of the exospore of mature *Marsilea* megaspores is very complex. Immediately overlying the endospore is the inner division of the exospore which Feller (1953) and Boterberg (1956) call the " reticulated layer ". This layer is continuous around most of the megaspore but gradually thins and disappears in the region of the germinal sutures. The " prismatic layer " forms the outer division of the exospore and also the outer layer of the megaspore exine *sensu stricto*. Both authors give a precise and detailed account of the development of the " prismatic layer " in *Marsilea* and the reader is directed to their publications for this information. In mature megaspores the " prismatic layer " consists of a basement membrane upon which is arranged a number of radially-directed elements that, under high magnifications, can be resolved as small prismatic chambers. According to Boterberg (1956) the chambers are open to the outside and during development are penetrated by digitations of the tapetal periplasmodium. Towards the spore apex the " prismatic layer " decreases in thickness and is not developed in the region of the germinal sutures.

The value of Ehrlich's haematoxylin and Orange G, Congo red, Fast green and Analine blue used by Feller (1953) and Boterberg (1956) in detecting the first appearance and subsequent deposition of sporopollenin in the wall layers is very limited. For example, Boterberg (1956) states that in mature or almost mature megaspores the " reticulated layer " is stained by Fast green, Analine blue, Congo red and Orange G. None of these stains is specific or even selective for lipoidal substances. The electron micrographs published here (Pl. 8, fig. 2) show that the " reticulated layer " in acetolyzed megaspores of *Marsilea quadrifolia* L. is composed of anastomosing rodlets of acetolysis-resistant material, and that the spaces between could have been occupied by some material that did not survive acetolysis. It is not impossible that the stains employed by Feller and by Boterberg are in fact colouring some interstitial substance between the sporopollenin elements rather than the exine material proper, even assuming that this had in fact been formed.

It is a well known fact that in the megasporangium of *Marsilea* only one fertile spore is produced. Although all the sporocytes in the megasporangium undergo meiosis, only a single spore from one of the tetrads so formed develops to maturity ; the remainder abort. Both Feller (1953) and Boterberg (1956) give an account of this very interesting phenomenon. They find that the three abortive spores that remain attached to the developing megaspore are surrounded by a membrane, the endospore, which is formed at the same time as the endospore of the fertile megaspore. Wall layers external to the endospore are not formed around the abortive members of the tetrad.

Acetolyzed megasporangia from mature sporocarps of *M. quadrifolia* and *Marsilea drummondii* A. Br. yield megaspores which often bear small acetolysis-resistant bodies attached at the apex (Pl. 9, figs. 1, 2). This situation is very reminiscent of that seen in the Devonian and Carboniferous megaspore tetrads of *Cystosporites*. Thin sections through the apical region of acetolyzed *M. drummondii* megaspores examined by phase contrast illumination (Pl. 9, fig. 2) show that the abortive spores are represented by small, irregularly-shaped masses of sporopollenin with small hollow vesicles, and appear very much as shown in the illustration of Boterberg (1956). There is none of the complex structural organization seen in the exine of the fertile megaspores.

Electron micrographs of ultra-thin sections through the exine of a fertile megaspore of *M. quadrifolia* illustrate that the exine stratification detected by Feller and by Boterberg in the megaspores of *M. hirsuta* and *M. diffusa* is the same in this species.

The inner layer of the exine (endexine) which is equivalent to the outer endospore of Feller and Boterberg is composed of sporopollenin which exhibits a granular structure in sections stained with potassium permanganate. On the inner border of this layer is a zone which is slightly more electron opaque than the remainder (Pl. 8, fig. 2).

The " reticulated layer " of the French authors is seen in electron mircographs to be composed, as mentioned above, of anastomosing rodlets of sporopollenin (Pl. 8, figs. 2, 3). The rodlets are more or less circular in cross-section and are surrounded by clear spaces that in the living spore were presumably filled with some interstitial substance. At the junction of the "reticulated layer" and the subjacent endexine the rodlets of the former are seen to arise directly from the somewhat irregular surface of the latter. There is thus structural continuity between the endexine and the innermost layer of the ektexine.

The most clear indication of the structural organization of the " prismatic layer " is obtained from thin sections examined by phase contrast illumination (Pl. 8, fig. 4). The outer terminations of the radially-directed chambers are seen to be covered by a thin, continuous, acetolysis-proof membrane. A membranous cover closing the prismatic chambers was not detected in *M. hirsuta* (Feller 1953) nor in *M. diffusa* (Boterberg 1956). The radial walls of the chambers are perforated with small, irregularly-shaped apertures which in sections of non-acetolyzed material are somewhat obscured by aggregations of small phase-dark granules adhering to the walls. There is some visual evidence to suggest that at their innermost limit the walls of the prismatic chambers divide, although the junction between the " prismatic layer " and the " reticulated layer " appears quite distinct under the optical microscope (Pl. 8, fig. 4). Electron micrographs of this region show, however, that the elements of the " prismatic layer " are in places continuous with those of the " reticulated layer " (Pl. 8, fig. 3). The fine structural continuity between the three layers comprising the megaspore exine of *M. quadrifolia* suggests perhaps that sporopollenin deposition in the megasporangium is a continuous process. The implication here is that the very marked stratification in the megaspore wall of this genus does not necessarily mean that waves or cycles of sporopollenin deposition are separated by intervals when the mechanism, or mechanisms, responsible for wall formation is inactive.

Microspores of Marsilea. Electron micrographs of radial sections through acetolyzed spores from the microsporangia of *M. quadrifolia* and *M. drummondii* clearly show the so-called " striated " or " prismatic " layer of the exine detected by Feller (1953) and Boterberg (1956). Tangential sections through this layer reveal, however, that the striations are in fact a system of more or less radially-aligned tubes (Pl. 9, fig. 5) that are closed at their apices, but interconnected at their bases (Pl. 9, fig. 4). The inner exine layer (endospore of Feller and Boterberg) appears to have a finely granular ultrastructure.

Both these authors in their respective accounts of microsporogenesis in *Marsilea* show that the microsporangia contain; in addition to the normal and presumably fertile microspores, a variable number of abortive spores. Perhaps the most interesting of these from a morphological point of view are the pseudospores. Pseudospores are described as anucleate, aplasmic spore-like inclusions that develop within small vacuoles in the tapetal periplasmodium. Their formation begins with droplets, which Bonnet (1955) identifies as tannoids but which Feller's evidence would suggest are sporopollenin, becoming surrounded by a thin, sudanophilic membrane. As development proceeds the surrounding membrane assumes an appearance very reminiscent of the outer membrane of the microspores. The final stage of pseudospore development is marked by the formation of one or more gelatinous layers on the outside of the " striated " layer. Feller (1953) recognizes four types of pseudospores that are separable on the form of the central inclusion, and there are structural intermediates between the four types. None of these contains a nucleus or cytoplasm and they do not appear to form in tetrads.

" Microspores volumineuses " are a second type of abnormal spore described by Feller (1953) and Boterberg (1956) but these, unlike the pseudospores, are formed from the archesporium. Their formation is due to a blockage in meiosis at or before metaphase II (Boterberg 1956), with the result that individual haploid microspores are not formed. " Microspores volumineuses " are, therefore, diploid, but the French authors find that exine development proceeds more or less normally and eventually the diploid spores are surrounded by a sudanophilic wall consisting of a thick endospore and a thinner " striated " overlying membrane. In the space between these two layers are small droplets of various shapes and sizes.

Acetolyzed microsporangia of *M. quadrifolia* and *M. drummondii* have been found to contain a large number of spores which from their structure when examined as entire objects could be equated with one or other of Feller's (1953) four types of pseudospores (Pl. 10, fig. 1). Examination of thin sections of these structures with anoptral contrast illumination suggests that the situation in my material cannot be fully explained on the basis of the interpretation of pseudospore formation given by Feller.

The sections show that each pseudospore is surrounded by an outer exine layer composed of radially-aligned tubes which seem to be exactly similar to the outer membrane of the normal, fertile microspores (Pl. 10, figs. 3–8). There is, however, considerable variation in the extent to which the inner wall layer is developed. In some of the smaller pseudospores it is not present as a distinct membrane but is represented merely by small, discrete, phase-white droplets of acetolysis-resistant material adhering to the inside of the external layer. The partial or nearly complete coalescence of these droplets in some specimens appears to result in a structure not unlike a membrane (Pl. 10, fig. 4). In somewhat larger pseudospores the inner layer can be seen as either a small central body having no structural connexion with the outer layer (Pl. 10, fig. 5) or as a much folded membrane that has contracted away from the outer layer (Pl. 10, figs. 7, 8). In both these forms (some specimens of which may be " microspores volumineuses ") small acetolysis-resistant, phase-white droplets are attached to the inner surface of the outer membrane. Pl. 10, fig. 6 shows a section of a spore the wall of which seems to differ from the normal condition (Pl. 10, fig. 3) only in the slight thickening of the inner layer and the partial contraction of this layer away from the external layer of the exine.

It should perhaps be emphasized here that the abnormal spores or pseudospores constitute the greater part of the contents of the microsporangium of *M. quadrifolia* and *M. drummondii*. The sections of these structures show that in all of them, no matter how contorted the inner membrane may be, a central lumen is always present. Cytoplasmic contents could not, however, be detected in the sections of non-acetolyzed material treated with appropriate nuclear and cytoplasmic stains. Nevertheless, the presence of a central lumen would seem to suggest, although not prove, that at some time they did possess cytoplasmic contents.

The evidence available from the sections indicates that the abnormal spores have to some extent followed the same developmental pattern as the fertile spores, but that at some stage during their development the process of wall formation has deviated from the normal. There are several relevant factors to be considered in this connexion. Firstly, both the normal and abnormal spores occur together in the same sporangium. Secondly, in all cases it seems to be only the inner exine layer of the abnormal spores that is malformed ; the outer membrane is precisely the same as in the normal spores. Electron micrographs confirm the optical observations on this point. Finally, the outer wall layer often assumes a shape that is quite independent of that assumed by the inner membrane.

Feller (1953) and Boterberg (1956) have found that in the development of the normal microspores the endospore is the first layer formed around the protoplast. If it can be assumed that this is also true for the abnormal spores then the endospore in these must have been formed around either a normal protoplast which subsequently degenerated or a protoplast that was degenerate from the start. The fact that the outer membrane in these spores is completely normal and does not necessarily follow the contours of the endospore would seem to lend support to the first alternative. However, there are points which still remain to be explained. Whilst the degeneration and subsequent contraction of the protoplast could be responsible for the collapse of the endospore it is difficult to see how it could account for the increased thickness of this layer in the abortive spores. The presence of acetolysis-proof droplets which may represent the inner layer in some spores and those that occur between the two wall layers in others also needs to be explained.

It is difficult to reconcile Feller's (1953) interpretation of the origin and mode of development of aplasmic, anucleate pseudospores with the level of structural organization revealed in the abortive spores described above. Heslop-Harrison (1963*a*, *b*) has shown that the protoplast of pollen grains is involved in the establishment of the exine pattern and it is of more than local interest to establish precisely how the spore wall is formed in the abortive microspores of *Marsilea*, and at what stage during the process the spore protoplast begins to degenerate.

One further point should be mentioned here. Feller (1953) and Boterberg (1956) refer to small granules of material, which chemically resemble the exine substance, occurring in blebs that arise from the tapetal periplasmodium adjacent to the developing microspores. Feller, who follows their development, believes that these granules contribute towards the formation of the microspore exine. The granules may well be identical with the Ubisch bodies described by Rowley (1963) or the tapetal plaques detected by Heslop-Harrison (1962, 1963*b*) in the pollen sacs of angiosperms.

Shattuck (1910) described how the degree of spore abortion in the sporangia of *Marsilea* can be controlled by varying the external conditions under which the plants are growing. He shows that there is some correlation between the time during spore development at which the stimulus (a change in temperature or light intensity) is applied and the resultant fertility of the spores. The critical period in this respect would seem to be from the time the mother cells enter synapsis until the tetrads are well formed. Shattuck advances the suggestion that a mechanism of this sort could have been responsible for the origin of heterospory in *Marsilea* and possibly for its origin in all heterosporous plants. By varying the external conditions and reducing the number of developing sporocarps on a plant Shattuck was able to induce the formation of large spores or " megaspores " in microsporangia and small spores or " microspores " in megasporangia. Shattuck is not unaware of the very significant differences between heterospory and heterothally and he attempted, without success, to germinate the experimentally produced " megaspores " and " microspores ". Thus, the only reliable criterion that would test the validity of his claims, the production of megagametophytes and microgametophytes, could not be applied. Nevertheless, the possible significance of his observations cannot be ignored.

The megaspores of *Marsilea* have, unquestionably, the most complex exine structure of any megaspores from either living or fossil plants so far investigated. It is considerably more complex than that seen in the megaspores of the lycopods *Selaginella* and *Isoetes*. Although the exine structure of the microspores of *Marsilea* appears superficially similar to that of the megaspores, ultra-thin sections show that there is a large measure of difference between the two.

Megaspore of Regnellidium. Chrysler & Johnson (1939) describe the wall of the mature megaspore of *Regnellidium diphyllum* Lindm. as consisting of two principal layers, the endospore and the epispore ; the latter being subdivided into three sublayers. According to their interpretation the endospore lies next to the spore protoplast and is continuous under the apical papilla. The homogeneous inner layer of the epispore is sudanophilic, lies closely applied to the endospore and is not continuous under the papilla. The thickest layer of the megaspore wall is formed by the middle layer of the epispore, the prismatic layer. This is composed of hollow radiating chambers or prisms the outer ends of which are closed by a membranous cap. The prismatic layer is also sudanophilic. The outer layer of the epispore is termed the papillate layer but since microchemical tests show it to be composed of cellulose it will not be considered further. Finally, a thick layer of mucilagenous material was detected between the papillate layer and the sporangium wall, but the authors do not regard this as part of the megaspore wall.

Although Chrysler & Johnson (1939) do not record the presence of a layer internal to the endospore in the megaspores of *Regnellidium* they do illustrate sections of spores which clearly show a membrane in this position and which they regard as a layer of the cytoplasm. This layer is continuous over the floor of the papilla and appropriate histochemical tests would determine whether it is analogous to the intine of angiosperm pollen.

The megaspore wall of *Regnellidium* has not so far been examined in the electron microscope, but sections of acetolyzed material examined by phase contrast microscopy show that the exine stratification, although somewhat similar to that of *Marsilea* megaspores, differs sufficiently to warrant description.

Under phase contrast the inner layer of the megaspore wall (endexine or endospore of Chrysler & Johnson) appears to be homogeneous (Pl. 10, figs. 9, 10). The layer immediately overlying the endexine (inner layer of the epispore of Chrysler & Johnson) is not homogeneous, but structurally resembles the " reticulated layer " of *Marsilea* megaspores. In *Regnellidium*, however, the " reticulated layer " is thicker than in *Marsilea* and subdivided into two very distinct zones, the outer one of which has a coarser structure than the inner (Pl. 10, fig. 10).

In the megaspores of *Marsilea* the radially-arranged hollow chambers or prisms are covered by a continuous membrane which passes without interruption across their outer surfaces. In *Regnellidium* the situation is somewhat different. The membrane terminating each chamber is not continuous and the result, as Chrysler & Johnson (1939) point out, is that the outer surface of the layer appears papillate (Pl. 10, fig. 9). Enclosed at the outer end of each of the chambers is an accumulation of acetolysis-resistant material in the form of small phase-dark granules.

The microspore of *R. diphyllum* is, according to Chrysler & Johnson, a small edition of the megaspore. Two wall layers can be detected, an endospore and an outer prismatic layer. The authors observed several cases where the prismatic layer surrounded an entire tetrad of microspores or, in some cases, possibly even two tetrads.

SPORES OF LIVING AND FOSSIL HOMOSPOROUS PTERIDOPHYTES

The spores of three genera of living homosporous pteridophytes (*Lycopodium*, *Psilotum* and *Asplenium*) have been examined to determine how the exine of these spores compare with the microspores of living and fossil heterosporous pteridophytes. In addition, one fossil dispersed spore from the Devonian (*Archaeotriletes*), the parent plant of which is unknown but is assumed to have been homosporous, has been sectioned.

Spores of *Lycopodium*

The electron micrographs of acetolyzed and chlorinated *Lycopodium clavatum* spore walls published by Afzelius, Erdtman & Sjöstrand (1954) show that the exine is divided into an outer lamellated and an inner granular layer. Afzelius (1956) shows how the fine structure of the spore exine can be destroyed by over-chlorination or treatment with chromic acid.

Acetolyzed spores of *Lycopodium selago* L. (Pl. 10, fig. 11 ; Pl. 11, fig. 1) do not display the striking lamellation detected in the spores of *L. clavatum*, and the exine appears to be more or less granular to faintly fibrous. On the proximal side of the spores a discontinuous granular zone underlies the outer wall layer and this is ultrastructurally similar to the granular layer illustrated by Afzelius, Erdtman is Sjöstrand (1954). The rather irregular occurrence of the layer in *L. selago*, however, suggests that it is produced by the breakdown of the outer wall layer and should not be regarded as a separate stratum of the exine in these spores.

The fine structure of the spore wall in *L. selago* differs sufficiently from that detected in *L. clavatum* to justify an investigation to determine the full range of variation within the genus.

Spores of *Psilotum*

An acetolyzed exine of a *Psilotum nudum* Griseb. spore section stained with lead hydroxide is shown on Pl. 11, fig. 3. It can be seen that the wall is weakly stratified. A finely granular layer surrounds the spore lumen and to the outside is a somewhat thicker fibrous stratum. The undulating outer and inner margins of the wall have borders of rather higher electron density than the rest of the exine.

Spores of *Asplenium*

The spores of the polypodiaceous fern genus *Asplenium* have, according to Bower (1923) and Sorsa (1964) a distinct perispore or perine. The perispore is regarded as being the last layer formed by the tapetum. In the majority of species it is said to be represented by a thin, loosely-attached, often highly ornamented membrane (see, for example, Sorsa 1964). Erdtman (1952) does not consider the perispore as part of the exine in the strict sense, but rather as an extra-exinous layer of the sporoderm.

Electron micrographs of ultra-thin sections of acetolyzed spores of *Asplenium adiantum-nigrum* L. show that the wall is stratified into three distinct layers. The outer wall layer, or perispore, is very electron opaque. Stratification is clearly detectable within the perispore itself and is seen as a series of electron-dense membranes (two outer and two inner) enclosing two granular interstitial layers (Pl. 12, figs. 1, 2). The electron micrographs show that only the two outer perispore membranes and the outer granular layer that they enclose contribute to the formation of the elements which form the ornamentation of the spore. The two inner perispore membranes and the inner granular layer continue uninterrupted beneath the projections, and as a result they have a hollow central cavity.

Between the perispore and the inner layer of the spore wall is a space, the presence of which presumably accounts for the fact that the perispore is easily detached. The inner layer of the wall would constitute the whole of the exine *sensu stricto* according to Erdtman's (1952) generally accepted terminology for perinate spores. This layer in *A. adiantum-nigrum* is structurally homogeneous in most sections, but appears faintly granular in a few (Pl. 12, figs. 1, 2). The inner and outer edges of the layer are bordered by two very thin slightly more electron-opaque zones.

The exine fine structure of the spores of *A. adiantum-nigrum* is quite unlike the microspores of *Selaginella, Isoetes* and *Marsilea* or the spores of *Lycopodium* and *Psilotum.* By definition the perine of the *Asplenium* spores is a wall layer which has no homologue in these species, but this interpretation can be questioned and is discussed later. The fact that the inner wall layer or exine of the *Asplenium* spores is homogeneous and completely undifferentiated is not altogether a surprising discovery. Any discussion as to its possible significance would, however, be almost valueless without substantially more information on the range of ultrastructural variation in fern spores, particularly in the phylogenetically more primitive genera.

The wall structure of *Archaeotriletes*

The fossil spores provisionally referred to this rather broad genus were isolated with 40% hydrofluoric acid from a sandstone of Upper Devonian age from Scaumenac Bay, Quebec, Canada.

The botanical affinity of the spores is not known, but they possess, in common with a number of other genera of the same age, an ornamentation which consists of appendages that terminate in grapnel-shaped hooks (see Naumova 1953). The exine of *Archaeotriletes* has not been studied as completely as some of the other spores described in this account, and the observations are included as a first assessment which may have to be modified later.

Ultra-thin sections of *Archaeotriletes* show that the outer part of the exine which forms the wall ornamentation is composed of anastomosing rodlets of sporopollenin similar to those seen in the spores of *Archaeopteris*, the megaspores of *Selaginella* and *Isoetes* and the Carboniferous lycopod megaspore *Laevigatisporites*. The impression gained from some sections is that the orientation of the elements changes slightly towards the inside so that the wall appears to be weakly stratified (Pl. 12, fig. 4). So far a layer internal to the spongy layer has not been detected. Lastly, it can be seen that the spines which constitute the ornamentation of the spores are formed by the spongy layer and that they have a hollow central cavity (Pl. 12, fig. 3).

POLLEN OF FOSSIL AND LIVING GYMNOSPERMS

The exine structure of *Schopfipollenites*

Pollen belonging to the genus *Schopfipollenites* Potonié & Kremp 1954 was obtained from the Lawrence Shale, Lone Star Lake, Kansas. The Lawrence Shale is of Pennsylvanian (Virgillian) age.

Schopf (1949) has described pollen of the *Schopfipollenites* type in the medullosan pteridosperm fructifications *Dolerotheca* and *Whittleseya*, and there is no doubt that *Schopfipollenites* is a genus based on pollen. However, because the grains have both a proximal monolete aperture (a feature characteristic of some types of spores) and two distal grooves or sulci (a single sulcus is a feature characteristic of some pollen) Schopf has adopted Renault's term " prepollen " for the fossils. In view of Afzelius's (1956) suggestion that some submicroscopic features are more primitive than others it was considered of particular interest to examine the wall structure of *Schopfipollenites* by electron microscopy and to compare it with the structure detected in the microspores of the free-sporing vascular cryptogams and the pollen of living gymnospermous seed plants.

The exine of *Schopfipollenites* is divided into two very distinct layers which can be clearly seen with the optical microscope (Schopf 1949). In ultra-thin sections examined with the electron microscope the fine structural details of the two layers is resolved.

The inner exine layer (endexine) is distinctly lamellated (Pl. 13, figs. 2, 3 ; Pl. 14, fig. 1) but in places the lamellation is scarcely detectable doubtless as a result of compression during the fossilization process. In one section (Pl. 13, fig. 3) it appears as though the endexine is itself subdivided into two layers.

The outer layer of the exine (ektexine) is constructed of the familiar anastomosing units of sporopollenin giving the wall a spongy appearance. Structural distortion due to compression is also recognizable in this layer. Continuity exists between the endexine and the ektexine and in some of the micrographs (Pl. 13, fig. 2 ; Pl. 14, fig. 1) it can be seen that the innermost units of the ektexine arise directly from the outer surface of the endexine.

Towards the outer edge of the pollen grain the sporopollenin units of the ektexine are progressively more coalescent and at the periphery are completely fused to form a solid margin. Under the optical microscope entire specimens of *Schopfipollenites* from the Lawrence Shale appear to be minutely punctate (Pl. 13, fig. 1). The electron micrographs show, however, that the solid margin is not interrupted by punctae (Pl. 13, fig. 2). One possible explanation to account for this discrepancy is that the interstitial spaces between the outermost sporopollenin units of the ektexine can be mistaken for punctate surface ornamentation when the pollen is examined by transmitted light.

In the possession of a lamellated endexine and a spongy ektexine the exine of the pteridosperm pollen *Schopfipollenites* very closely resembles that of the spores of *Archaeopteris* and the megaspores of *Selaginella*. This fossil pollen is, in fact, ultrastructurally considerably more " spore-like " than " pollen-like ". This topic will be returned to later.

Pollen of *Encephalartos*

Sections of acetolyzed pollen from the living cycad *Encephalartos villosus* Lem. clearly show that the exine is stratified into three distinct layers.

The proximal surface of the grain is covered by an outer ektexinal layer of homogeneous to faintly fibrous sporopollenin that extends laterally round the sides of the grain and enters the distal sulcus where it rapidly thins and finally disappears (Pl. 15, figs. 1, 2). The inner and outer margins of this layer are interrupted by small cavities or pits (Pl. 14, fig. 2). Immediately underlying the outer ektexine is the middle wall layer or inner part of the ektexine which in thin sections appears to be prismatic. This layer is not well developed on the proximal face of the grain, but becomes thicker towards the sides and is thickest in the distal sulcus where, with the disappearance of the outer ektexine, it is the outer layer (Pl. 15, figs. 1, 2). In sections that pass obliquely through the inner ektexine it can be seen that the elements forming the layer are a system of radially-aligned closed tube-like processes. The outer extremities of the elements are connected to the inner surface of the outer ektexine, and the inner extremities to the innermost exine layer. In the distal sulcus, where the outer ektexine is not formed, the elements of the middle layer are terminated by a thin, continuous membrane which passes across their outer ends. This membrane could be considered to represent the outer ektexine in this region.

The endexine in *E. villosus* pollen is a very thin lamellated layer (Pl. 14, fig. 2). Not infrequently, the endexine and the inner ektexine become detached from the outer ektexine at the sides of the pollen grain so that they curve into the pollen lumen ; the effect is to make the grain appear saccate (Pl. 15, fig. 1).

Afzelius (1956) and Ueno (1960) have published electron micrographs showing the exine structure in the pollen of *Cycas*. Afzelius finds that the pollen exine of *Cycas revoluta* is composed of two layers, the inner layer being lamellated and the outer one being composed of branched bacula-like elements. Ueno, on the other hand, detected three layers in the pollen exine of *Cycas taiwaniana* which appear to correspond to the three layers in the pollen of *E. villosus*, although there are some small differences. The stratification in the pollen wall of *Ceratozamia mexicana* described by Larson (1964) closely resembles that found in *Cycas*. In *C. mexicana* also the innermost layer of the exine is lamellated.

Compared with the Carboniferous pteridosperm prepollen *Schopfipollenites* the exine stratification revealed in the pollen of living cycads is quite complex. One notable feature shown by Ueno's (1960) illustrations of *C. taiwaniana* and those of *E. villosus* illustrated here (Pl. 14, fig. 2 ; Pl. 15) is that the exine of cycad pollen grains is thinner in the distal sulcus or germinal furrow than in the rest of the wall. But this is not so in *Schopfipollenites*. Perhaps the distal sulci in the pteridosperm prepollen are not true germinal furrows but merely a harmomegathic region and germination may have occurred through the proximal suture, as in the spores of free-sporing pteridophytes.

Pollen of *Taxus*

In glutaraldehyde-fixed pollen of *Taxus baccata* L., post-fixed in osmium tetroxide, almost the entire thickness of the exine is conspicuously lamellated (Pl. 16, figs. 2, 3). On the outside of the lamellated layer is a zone rather than a uniform layer consisting of small, electron-dense droplets of exine material. Erdtman, Berglund & Praglowski (1961) call these structures orbicules, and they undoubtedly account for the pollen wall ornamentation. The orbicules vary somewhat in size and many bear small conical projections which radiate from their surfaces. The arrangement of these bodies on the surface of the lamellated layer seems to be quite haphazard. Some lie directly on the lamellated layer and in close contact with adjacent orbicules so that there is a suggestion of partial coalescence between them. Others lie completely free and some distance above the lamellated layer. At high magnifications a substance with a granular fine structure can be detected between the orbicules and the lamellated layer. This substance appears to bind the innermost orbicules to the subtending layer and in some cases to cement the orbicules together (Pl. 16, fig. 2).

Between the lamellated layer and the pollen cytoplasm is a fairly thick, electron-transparent intine which is structureless in material fixed in glutaraldehyde and post-fixed in osmium tetroxide.

Ueno (1959) considers the small spinous droplets covering the *Taxus* exine as perine which is united with the outer exine layer or sexine. The sexine is the name applied by Ueno to the granular substance situated between the droplets and the lamellated layer. Certainly, the very scattered distribution and somewhat irregular appearance of the orbicules are very unusual features which perhaps have their nearest homologue in the perispore of the pteridophytes rather than in a true exine layer. Of some significance in this connexion are the small electron-dense droplets which occur in the innermost pollen sac tapetal cells of *Taxus*. These droplets closely resemble those attached to the pollen exine (Pl. 16, fig. 4). Similar droplets also occur between adjacent pollen grains and seemingly lie free in the pollen sac locule. They can be compared with the Ubisch bodies described by Rowley (1963) and the tapetal plaques of Heslop-Harrison (1962, 1963*b*). Sporopollenin droplets of this kind are not confined to *Taxus* and Ueno (1959) has shown that they occur in a number of other coniferous genera. Afzelius (1956) also draws attention to their presence in *Cephalotaxus*. There is also some apparent structural homology between these structures in the conifers and those that form the outer layer or zone of the spore wall in the moss *Dicranum scoparium* Hedw. described below.

Pollen of *Pinus*

The ultrastructure of the pollen wall of *Pinus* has been described by Mühlethaler (1955), Ueno (1958) and by Ting & Tseng (1965). The electron micrographs of exine structure in *Pinus balfouriana* published by the latter authors show that the inner wall layer (endexine) in this species is granular in composition. Overlying the endexine is a thicker ektexine which they subdivide into a " foot layer " or " limen inferum ", a series of columellae with " depressions " and " funnels " and a tectum. Their pictures show that the ektexine expands to form the sacci of the pollen grain whilst the granular endexine alone remains to form the floor of the sacci. In contrast to this, Ueno (1958) has shown that in *Pinus thunbergii* only the tectum and the columellae contribute to the sacci, and the saccus floor is formed by the " foot layer ". This also seems to be the case in *Pinus nigra* (Mühlethaler 1955).

Sections of *Pinus sylvestris* L. pollen that has been fixed in glutaraldehyde and post-fixed in osmium tetroxide show features which are structurally in accord with those published by Ueno (1958) in *P. thunbergii*. The inner layer of the exine (endexine) in *P. sylvestris* is composed of lamellated sporopollenin (Pl. 17, fig. 4). An ektexine overlies the endexine and consists of a basal layer (" foot layer "), a series of columellae which are sometimes branched (termed the " tigna " by Ting & Tseng 1965) and a tectum. The tectum is folded in places and possibly interrupted by " depressions " and " funnels " similar to those detected in *P. balfouriana* by Ting & Tseng (Pl. 17, fig. 3). The basal membrane (" foot layer ") of the ektexine appears to be composed of a series of distinct droplets of the exine material which lie in close contact and which, in places, are partly coalescent. However, it seems likely that the droplets are arranged along a thin and continuous membrane which they are obscuring (Pl. 17, fig. 4).

One notable feature is the difference in the construction of the sacci in *P. sylvestris* and in *P. balfouriana*. In the former, unlike the latter, the saccus is composed only of the columellae and the tectum of the ektexine (Pl. 17, fig. 2 ; Pl. 18, fig. 1), the inner layer or " foot layer " has not expanded but remained to form the floor of the saccus precisely as in *P. nigra* (Mühlethaler 1955) and *P. thunbergii* (Ueno 1958).

Another marked difference between the two species is in the fine structure of the endexine. In *P. balfouriana* it is granular, in *P. sylvestris* it is distinctly lamellated. Although Ueno (1958) does not comment directly about the structure of this layer in *P. thunbergii*, judging solely from his drawings it appears to be lamellated.

The structural variation of the endexine in the pollen of *Pinus* could be of taxonomic and possibly of phylogenetic importance, and a full comparative ultrastructural investigation into the wall structure of both living and fossil species would be worthwhile.

Lastly, and merely to record the observation, Ubisch body-like objects can also be detected adjacent to the tapetal cell walls in *Pinus sylvestris* pollen sacs (Pl. 18, fig. 2).

THE MEGASPORE MEMBRANE OF PALAEOZOIC SEEDS AND SEED-LIKE STRUCTURES

It has already been pointed out that the structure of the megaspore membrane in some Carboniferous cordaite and pteridosperm ovules is very different in construction from that of the ovules of living gymnosperms (Pettitt 1966). The observations described below present the evidence in support of this statement.

The megaspore membrane of Carboniferous cordaitalean and pteridosperm ovules

The cordaitalean ovules from which the megaspore membranes used in this study were obtained occur as compression fossils in the Lawrence Shale (Virgillian) of Lone Star Lake, Kansas. The cuticle morphology of the ovules (to be described elsewhere) is very characteristic and leaves no doubt that they are cordaitalean. The pteridosperm megaspore membranes were isolated with hydrofluoric acid from " nucule " casts of *Trigonocarpus* from the British Coal Measures.

Ultra-thin sections of a methacrylate-embedded cordaite megaspore membrane from the Lawrence Shale are shown on Pl. 19, figs. 1–3. It can be seen that the entire thickness of the membrane is composed of a three-dimensional network of sporopollenin elements giving a spongy appearance. At higher magnifications (Pl. 19, fig. 2) the homogeneous structure of the elements is apparent. At the inner edge of the membrane, in contrast to the outer, the sporopollenin units are fused to form a distinct margin around the lumen (Pl. 19, fig. 3).

The very real structural resemblance of the megaspore membrane of these fossil ovules to the wall structure detected in the megaspores of *Selaginella*, the spores of *Archaeopteris* and the Carboniferous lycopod megaspore *Laevigatisporites* is of considerable interest. A repetition of this structure in the megaspore membrane of *Trigonocarpus* (Pl. 18, fig. 3) the ovule of a Carboniferous pteridosperm and in *Taxospermum*, a petrified cordaitalean ovule (Pl. 18, fig. 4) adds significantly to the statement that structurally the megaspore membranes of the early seed plants more closely resemble the spores of the free-sporing heterosporous pteridophytes than the megaspore membranes of the modern gymnosperms (Pettitt 1966). The phylogenetic significance of this is discussed below.

Megaspores of *Lepidocarpon*

Megaspore tetrads belonging to the genus *Cystosporites* are known to occur in the Carboniferous seed-like structures *Lepidocarpon*, and there is a great deal of evidence to suggest that all lepidocarp seeds contained tetrads of the *Cystosporites* type. Tetrads of *Cystosporites* are characterized by having one large, sac-like, presumably fertile spore and three, smaller, presumably abortive spores attached at the apex of the large one. It is quite probable that most species included in the genus do represent lepidocarp seed megaspores. Only the wall structure of the large fertile spore is described in this account.

Megaspore tetrads referable to *Cystosporites giganteus* (Zerndt) Schopf 1938 were isolated from a Lower Carboniferous coal from Fife in Scotland by digesting the matrix in dilute nitric acid. Chaloner (1952) has shown that megaspore tetrads of *C. giganteus* occur inside the lepidocarp seed *Lepidocarpon waltoni*.

The wall of the large spore of *C. giganteus* exhibits a very characteristic mesh-like or fibrous texture when examined in surface view with the light microscope (see Chaloner & Pettitt 1964). In contrast to this the walls of the three abortive spores appear to be homogeneous or faintly granular when examined in this way.

Examination of sections of the fertile spore by electron microscopy clearly reveals the arrangement and fine structure of the fibrils that compose the outer wall layer. It can be seen (Pl. 20, figs. 1, 2) that the elements form a lose-textured stratum. The electron micrographs show that there are two distinct sizes of fibrils. The larger ones are themselves fibrillar in structure, whilst the smaller ones are homogeneous and more or less circular in cross section. There is evidence from electron microscopy of sections and from phase contrast studies of the surface which suggests that the two types of fibrils are interconnected or that the large fibrous type branch and give rise to the smaller variety.

The inner layer of the *Cystosporites* exine is very thin and is composed of homogeneous sporopollenin (Pl. 20, figs 1, 2).

In his description of *Cystosporites* Schopf (1938) draws particular attention to the fibrous character of the fertile spore exine. He supposes that this type of structure is correlated with the passage of food reserves from the parent plant into the megaspore whilst it is enclosed in the sporangium and after the exine was formed. This interpretation would obviously not be applicable to those species of the genus, for example, *Cystosporites verrucosus* and *C. devonicus* (see Chaloner & Pettitt 1964) in which the exine is not fibrous but more compact and homogeneous. The spongy texture of the megaspore wall of *Laevigatisporites*, a sigillarian megaspore described earlier, is not without significance in this connexion. *Sigillaria* is a free-sporing heterosporous plant which had, presumably, an endosporic gametophyte that developed in much the same way as the present day *Selaginella* or *Isoetes*. Whilst the possible physiological significance of a porous megaspore exine surrounding the female gametophyte of *Cystosporites* can be appreciated, that of an equally porous membrane surrounding the gametophytes of *Selaginella*, *Isoetes* and *Laevigatisporites* is not so readily apparent.

The exine structure of *Didymosporites*

The inclusion of an account of the exine of the fossil megaspore tetrads *Didymosporites* under the general heading of seeds and seed-like structures is not meant to imply that these tetrads are known to occur in seeds or even seed-like organs. However, it has been suggested by some authors (see Andrews 1961) that the Lower Carboniferous fossil *Bensonites*, the parent sporangium of *Didymosporites* (Chaloner 1958), may represent a morphological stage intermediate between heterospory and the seed habit. For this reason, as well as that of convenience, the account has been included at this point.

Tetrads of *Didymosporites* are composed of two large, thin-walled, presumably fertile spores and two minute, presumably abortive ones that are situated at the junction of the two large spores (Pl. 21, fig. 4). Chaloner (1958) has isolated *Didymosporites* tetrads from the megasporangium (*Bensonites fusiformis*) of the Lower Carboniferous coenopterid *Stauropteris burntislandica*. He also obtained tetrads of *Didymosporites* (*D. scotti*) from a Lower Carboniferous (Dinantian) coal outcropping east of Pittenweem Harbour in Fife, Scotland and it was from this material that the megaspore tetrads described below were obtained.

The exine of the large, presumably fertile spores of *D. scotti*, when examined as thin sections with the electron microscope, are completely homogeneous and show no detectable stratification (Pl. 21, fig. 1). Anoptral contrast pictures of sections through the entire tetrad (Pl. 21, figs. 2, 3) show that the structural homogeneity extends throughout the fertile spore. The exines of the abortive spores are also homogeneous. A thin, structureless membrane surrounds each tetrad, and this presumably represents, as Chaloner (1958) suggests, a remnant of the tapetum.

IV. GENERAL DISCUSSION

The foregoing descriptions of the structure of the spore and pollen grain walls as revealed by the electron microscope show that there is a considerable amount of ultrastructural variation in the exines of the various genera and the question arises as to whether the observed structural variations have any phylogenetic significance, and to what, if anything, they can be attributed.

In their work on the structure of the spores of the Musci, McClymont & Larson (1964) find that the wall stratification in all the spores that they examined was basically similar. They also show that the exine of moss spores is rather more simple in construction than that of the vascular cryptogams described above. In the mosses they detected two exine layers, the inner of which is very thin and featureless. The outer exine layer is electron-opaque, acetolysis-resistant and appears to be homogeneous. This layer, according to the authors, corresponds to that which Afzelius (1957) has called the exine in *Funaria* spores. In the spores of some genera (e.g. *Physcosmitrium* and *Encalyptra*) this layer does not participate in the formation of the wall ornamentation, whilst in others (e.g. *Polytrichum* and *Astonum*) it forms either the entire sculptural element or only the base. In the latter case it seems that the major part of the sculptural element is composed of a third layer which McClymont & Larson call the perine. It is also suggested that the perine forms the entire sculptural element in those spores where the exine takes no part in the formation of the wall ornamentation (e.g. *Physcosmitrium* and *Encalyptra*).

Electron micrographs of acetolyzed spores of the moss *Dicranum scoparium* are shown on Pl. 20, figs. 3, 4. In these the exine is composed of a homogeneous to faintly granular layer which bears on its outer surface a number of irregularly arranged and variously shaped droplets that represent the wall ornamentation. These elements closely resemble those which McClymont & Larson (1964) refer to as perine. Low magnification pictures of sections through an acetolyzed capsule of *Dicranum* (Pl. 20, fig. 4) show that the droplets are not only arranged on the spore exines but also randomly distributed in the spaces between the spores and are concentrated in a narrow zone adjacent to the remnants of the capsule wall. The occurrence of the droplets adjacent to the capsule wall strongly suggests that they were in some way associated with the tapetal tissue which has, of course, been destroyed by acetolysis. If these droplets do in fact originate from the tapetal cells, then McClymont & Larson's suggestion that they are perinous (*sensu* Erdtman 1952) would be strictly correct. There is an unescapable resemblance in the arrangement and occurrence of the droplets forming the spore ornamentation in the mosses and the droplets associated with the pollen wall of *Taxus baccata* described earlier (p. 245) and which Ueno (1959) regards as being a perine.

Before continuing there is perhaps some justification for discussing the precise interpretation of the perine. The term perine (or one of its synonyms) has been applied to a variety of exinous or extra-exinous layers of the spore or pollen wall with, seemingly, very little concern as to whether the layer in question is truly perinous. Arising from this is a more important issue; whether all the layers to which the term has been applied are homologous.

Erdtman (1952) regards the perine as an outer, extra-exinous layer of the spore wall of certain mosses and ferns which is formed by the activity of a tapetal plasmodium with "perinogeneous properties". He points out that it is virtually impossible to determine whether a particular layer is exinous or perinous without undertaking a study of the development of the spores.

Harris (1955) also discusses the origin of the perispore or perine and suggests that if the ornamentation of spores arises as a result of the periplasmodial substance gelling on the outer surface of the spore the layer thus formed is the perispore. This definition is essentially the same as that proposed by Bower (1923) and it would seem to restrict the use of the term perine to the spores from plants with a plasmodial tapetum. Rowley's (1963) observation that Ubisch bodies (tapetal plaques, tapetal droplets or orbicules) are apparently only formed in plants with a secretion tapetal system is very relevant in this connexion.

Bower (1923) considers that the most striking development of the perispore is in the Salviniaceae, and regards the massulae in the microsporangium and the glochidia and " swimming organ " of the megasporangia of *Azolla* as perispores with a specialized function. Eames (1936) on the other hand, restricts the term to the meshed structure formed around the megaspore by the fourth massula. Arnold (1955) has shown that this structure survives in fossils.

In the mature microsporangia of *Salvinia* the spores are surrounded by an amorphous mass of vacuolate, sudanophilic, acetolysis-resistant material (Pl. 21, fig. 5) which is formed from the tapetal periplasmodium. Eames (1936) calls this the perispore and, in the sense that this term is defined by Erdtman (1952) and Harris (1955) his usage is correct. A very similar vacuolate mass also occurs in the megasporangium of *Salvinia*.

Fitting (1900), as mentioned before, recommends that the term perispore should be applied only to wall layers that are formed from the special mother cell wall and the term epispore to those formed from the tapetum.

In the spores of *Asplenium adiantum-nigrum*, however, the outer layer of the wall or so-called perispore (see Nilsson & Praglowski 1963) appears, ultrastructurally, to resemble a true exine layer. It is difficult to believe that the perispore in *Asplenium* or in *Isoetes* microspores for that matter, originates directly from a periplasmodium by the process of gelling suggested by Harris (1955).

There is clearly a need for a full comparative developmental investigation into the formation of these wall layers. The correct interpretation can, as Erdtman has said, only be obtained from such a study. The results might well provide an explanation for the presence of the tapetal droplets in the pollen sacs of some conifers and in the capsules of mosses. It would surely clarify the situation with regard to the homology, if it exists, between the structurally distinct perispore in the Salviniaceae, the Polypodiaceae and the conifers and mosses. It might even result in a much-needed, clear and authenticated terminology!

Before leaving the question of tapetal derivatives, one further point is of particular relevance to the present study. It has already been shown (Pettitt 1966) that in certain gymnospermous ovules the structure which is called the megaspore membrane is, in fact, formed by the degeneration of the tapetum to form a thick, acetolysis-resistant membrane. The homologue of this tapetal membrane in the sporangia of free-sporing plants with a plasmodial tapetum would possibly be the perispore.

The tapetal membrane in the ovule would be, for example, homologous to the vacuolate sudanophilic mass of the *Salvinia* microsporangia and to the outer membrane of the spores of *A. adiantum-nigrum.* While there may be certain, admittedly somewhat tenuous, structural similarities between the tapetal membrane of the ovules and the perispore of *Salvinia,* there are less between the former and the perispore of *A. adiantum-nigrum.*

McClymont & Larson's (1964) study of moss spores shows that the exine in these plants is less well differentiated than it is in the vascular cryptogams. At the present state of our knowledge it is probably premature to discuss whether this means that they are also more primitive in an evolutionary sense. Such a discussion would have relatively little value until we are more sure of the criteria for judging the " simple " level of organization (as opposed to " reduced " and " derived ") in spore and pollen walls. If complex structural differentiation in the exine is a measure of phylogenetic advancement then the spores of the mosses, of *Psilotum, Lycopodium* and the microspores of *Selaginella* have a primitive exine structure ; certainly more primitive than the pteridosperm prepollen *Schopfipollenites,* for example.

Accepting Afzelius's hypothesis (1956) that pollen grains with a thin lamellated layer in the exine are phylogenetically more advanced than those with a thick lamellated layer, it is not surprising to find that the prepollen *Schopfipollenites* is phylogenetically less advanced than the pollen of *Encephalartos.* This hypothesis would, however, be difficult to apply in cases where an inner lamellated layer is not formed. In these spores the absence of such a layer could be taken to mean either that it has been completely reduced, and therefore the spores were advanced, or that it had not developed at all. It is not clear precisely how the microspores of *Isoetes,* with a well-developed lamellated layer as the outer wall stratum, would fit into this scheme, unless one accepts Nilsson & Praglowski's (1963) suggestion that this layer is the perine (and therefore not strictly part of the exine).

From a palaeobotanical standpoint one of the most interesting facts to emerge from the present study is that of the structural similarity between the megaspores of some of the free-sporing heterosporous plants and the megaspore membranes of the fossil gymnosperms. In the heterosporous Upper Devonian pteridophyte *Archaeopteris* the exine structure of the microspore and megaspore is almost identical. The situation is made the more striking by the structural dissimilarity of the microspores and megaspores in *S. pulcherrima.* It would be convenient, to say the least, to consider the spores of *Archaeopteris* as indicating that heterospory in this plant was not far developed from a homosporous stage and that the structure of the microspores and megaspores had not differentiated much beyond that of some ancestral isospores. This situation can be contrasted with the structure of the microspores and megaspores in *Selaginella,* a plant in which heterospory has long prevailed.

It would seem that there is some correlation between a spongy or fibrous exine structure and the retention of the female gametophyte within the megaspore. This type of wall texture is seen in the megaspores of *Selaginella, Isoetes,* in the Carboniferous spores *Laevigatisporites* and *Cystosporites,* and also in some Palaeozoic gymnosperm ovules. *Didymosporites* would appear to be an exception. At the risk of overstressing the significance of this it could be surmised that the continued evolution of a megaspore of the *Archaeopteris* type could result in further development of the spongy layer and the suppression of the inner lamellated layer. This process would result from, or accompany, the retention of the female gametophyte within the megaspore. The final structure would resemble the megaspore of *Selaginella*. Resulting from the retention of the megaspore within the megasporangium to form an ovule all that would be necessary to form a megaspore membrane of the type contained in the Carboniferous pteridosperms and cordaites is the complete suppression of the thin, inner, lamellated layer and a slight reduction in thickness of the spongy layer. It is worth repeating here that this structure is totally different from that found in modern gymnospermous ovules (Pettitt 1966). The hypothesis is, however, substantially weakened by the fact that a spongy exine is not confined to the spores of free-sporing heterosporous plants and the megaspores of fossil ovules. Larson (1964) has found that the ektexine of *Linum* pollen is composed of ramifying sporopollenin rodlets and this type of structure also occurs in the pollen of *Juglans* and *Carya* (Stone *et al.* 1964).

The structural similarity of the *Archaeopteris* exine and that of the Carboniferous prepollen *Schopfipollenites* suggests that very little, if any, fine structural alteration need accompany the change from microspore to pollen grain, if indeed such a change occurred. The comparison of the prepollen exine with that of the pollen from the living cycads and conifers shows quite clearly that the exine of the fossil is ultrastructurally considerably closer to a spore than to a pollen grain.

A spore-like exine structure can also be seen in the Carboniferous pollen *Florinites* (Pl. 19, fig. 4). This material was recovered as pollen masses from the same horizon in Kansas as the cordaitalean ovules. The genus *Florinites* represents the pollen of the cordaites and has been found in unquestionably cordaitalean pollen sacs by Florin (1936), Delevoryas (1953) and Fry (1956).

Sections through the central body of the grain show that it is composed of an outer spongy layer and an inner, much thinner, granular layer (Pl. 19, fig. 5). The inner layer shows no trace of lamellation.

The structural and/or physiological significance of an inner lamellated layer in the exine is some way from being understood, but Larson's (1964) discovery that the inner wall layer of *Bruchia brevifolia* spores is lamellated only in the harmomegathic region is of significance in this connexion.

It would be of considerable interest to know the implications of fine structural changes in the exine, and to establish precisely what is responsible for the observed differences. Judging from the very apparent dissimilarity of the microspores and megaspores of *S. pulcherrima*, for example, it might be supposed that the mechanism involved is very fundamental. It is noteworthy that Manton (1950) has shown that in forms of " *Cystopteris fragilis* " a difference in spore size can be correlated with a difference in chromosome number ; large spiny spores are associated with a high chromosome number ($n = 126$) and somewhat smaller spiny spores with a low chromosome number ($n = 84$). Examination with an electron microscope would show whether the difference here is purely one of spore size or if it extends to the wall structure.

A final comment of taxonomic interest arising from this study of spore and pollen wall structure must be included.

The separation of the inner exine layer or layers that was observed in the spores of *Archaeopteris*, *Selaginella* and *Isoetes* is clearly relevant to the correct interpretation of spore and pollen grain morphology, particularly in dispersed fossil specimens. Spores in which the inner layer of the exine is separated from the outer by a cavity are described as cavate (Dettman 1963, Faegri & Iverson 1964) and at least in some cases the inner layer or membrane is termed the mesospore (see Kremp 1965 : 89). Fitting's (1900) application of this term has already been fully discussed. The amount of variation that can occur in the formation of a mesospore, even in the spores of a single sporangium, is illustrated by the microspores of *Isoetes* (Pl. 7, figs. 1–8) and *Botrychium jenmanii* Underw. (Pl. 6, fig. 6), and there is certainly a need for caution in assessing the taxonomic value of such structural features.

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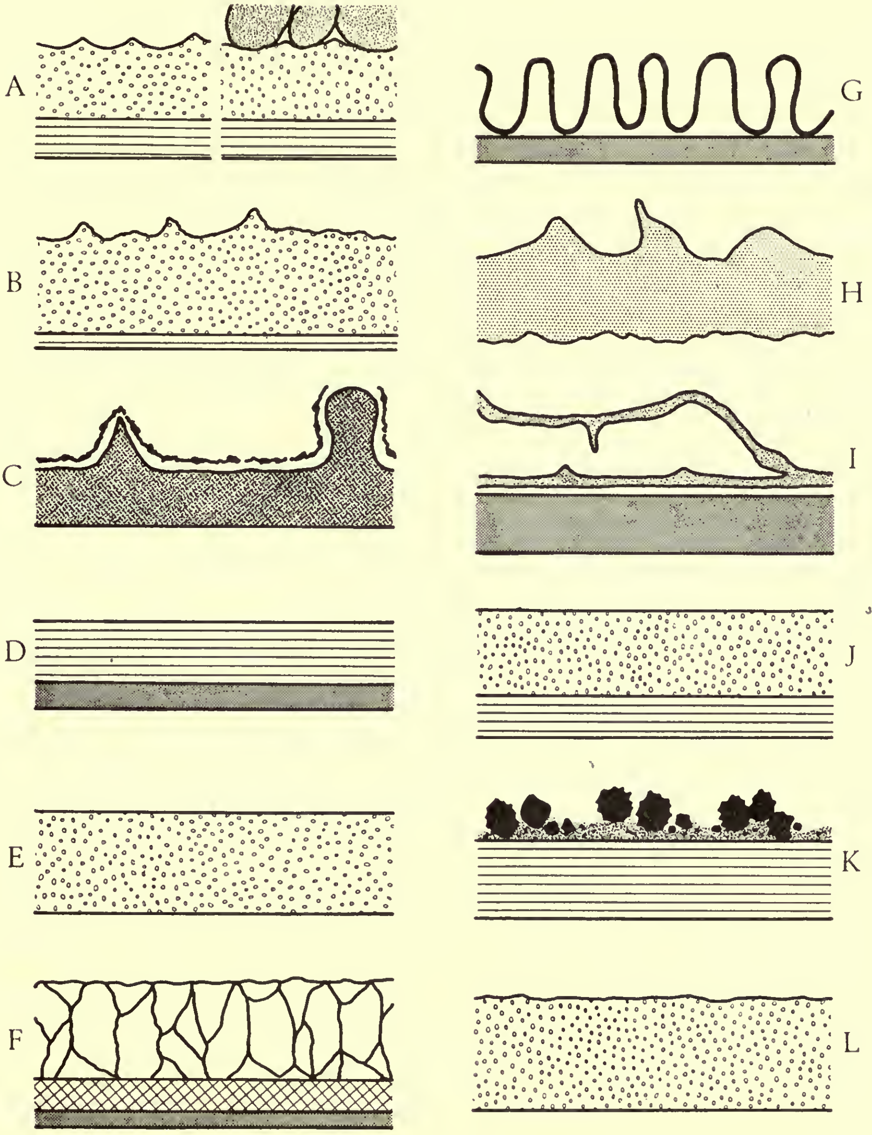

Fig. 1. Comparative diagrammatic drawings of exine stratification in : A, *Archaeopteris* microspores (left) and megaspores (right) ; B, *Selaginella* megaspores ; C, *Selaginella* microspores ; D, *Isoetes* microspores ; E, *Laevigatisporites* ; H, *Lycopodium* ; I, *Asplenium*; J, *Schopfipollenites* ; K, *Taxus* and L, a cordaite seed megaspore. The drawings are not to scale.

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PLATE 1

Selaginella pulcherrima (Megaspores) p. 227

FIG. 1. Section treated by periodic acid/Schiff procedure. Intine and thin membrane surrounding the spore protoplast coloured red. Spore protoplast is faintly pink. The exine is not coloured. ×400.

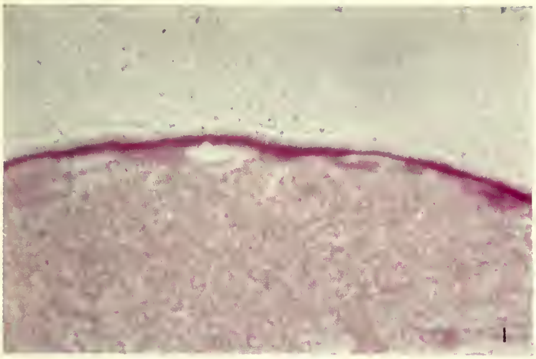
FIG. 2. Section treated by the periodic acid/Schiff procedure. The thin membrane (red) surrounding the spore protoplast is shown more clearly than in Fig. 1. ×425.

FIG. 3. Section treated by periodic acid/Schiff procedure. The inner, fibrous zone of the mesospore is coloured a vivid red. The outer, granular zone, is not coloured. ×460.

FIG. 4. Section treated by Nile blue sulphate method. Ektexine and outer, granular zone of mesospore stained blue. Inner, fibrous zone of mesospore very faintly coloured. ×157.

FIG. 5. Section stained with Sudan black B. The mesospore and the ektexine are strongly sudanophilic. ×390.

FIG. 6. Section stained with acetylated Sudan black B. Three sudanophilic membranes can be seen ; the ektexine (black arc at top of figure), the endexine and the one closely associated with the spore protoplast. The intine is not stained. Protoplast and inner wall layers have pulled away from the ektexine. ×685.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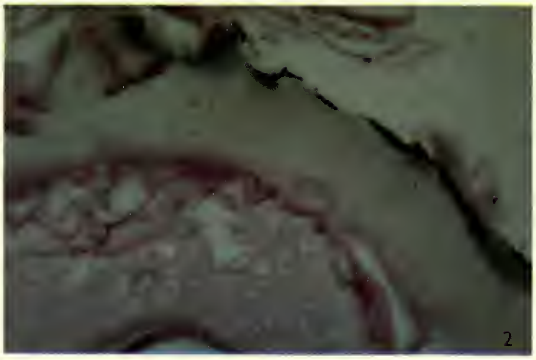
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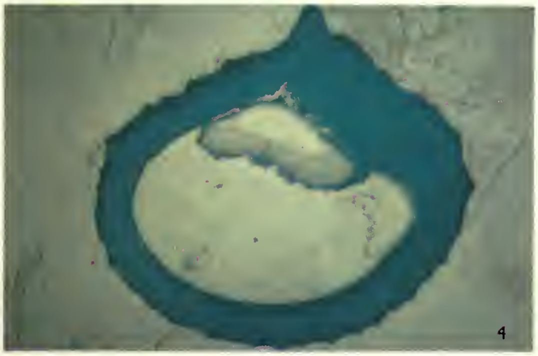
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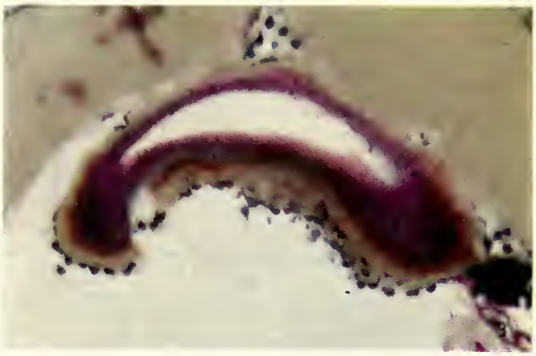
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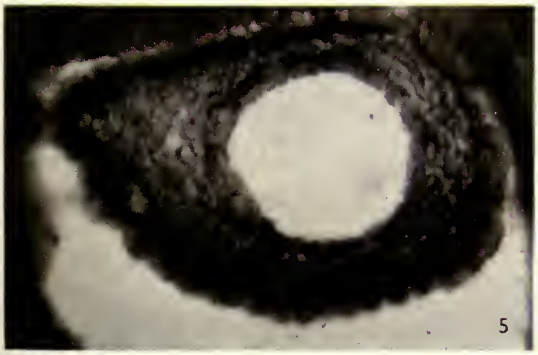
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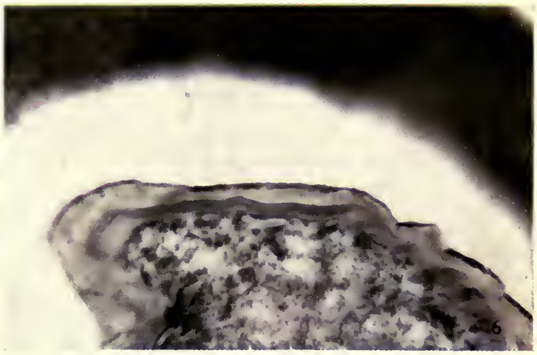
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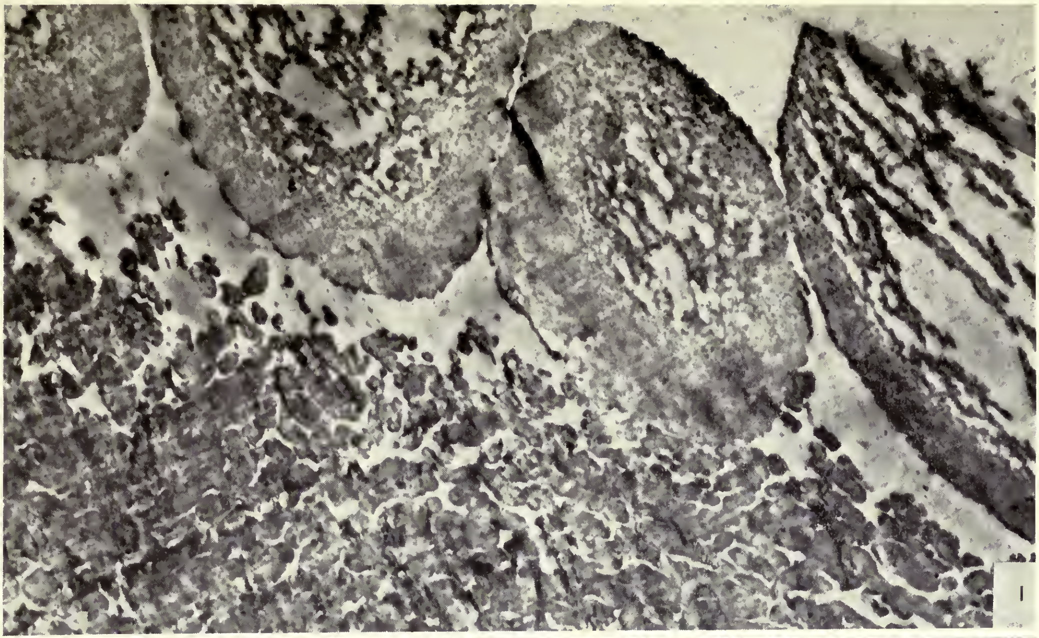
PLATE 2

Archaeopteris cf. ***jacksoni*** Dawson p. 225

FIG. 1. Outer part of megaspore wall showing associated spherical bodies. × 10,000.
FIG. 2. Inner part of megaspore wall. × 30,000.



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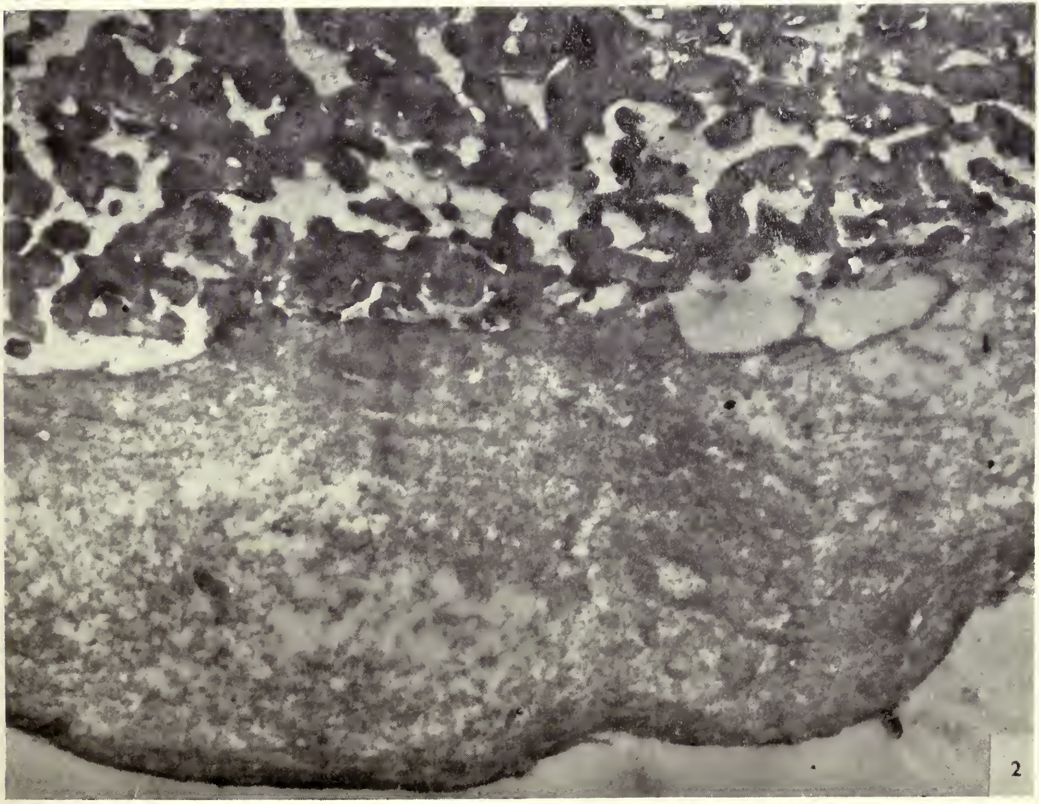

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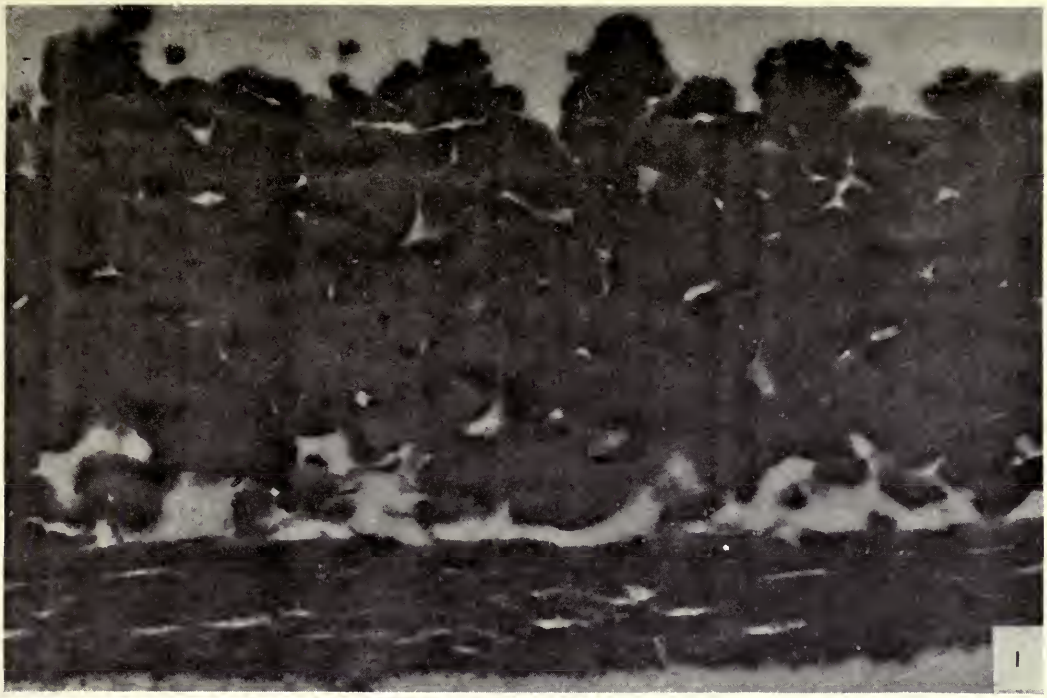
PLATE 3

Archaeopteris cf. ***jacksoni*** Dawson p. 225

FIG. 1. Section of microspore wall. × 30,000.

FIG. 2. Section of microspore wall passing through a commissure. The endexine passes upwards through the opening and overlaps onto the outer surface of the spore. × 7,500.

FIG. 3. Section of megaspore wall showing separation of the endexine into two layers. × 15,000.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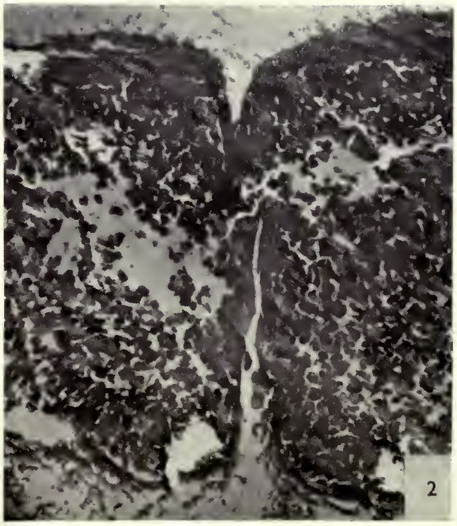
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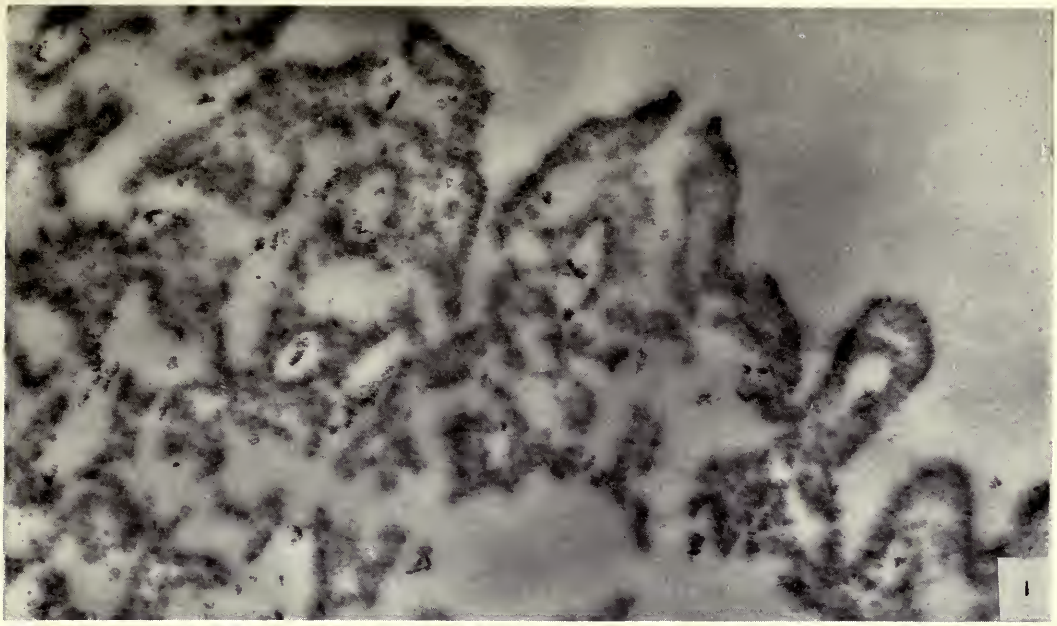
PLATE 4

Selaginella pulcherrima Liebm. p. 227

FIG. 1. Outer part of megaspore wall. ×25,000.

FIG. 2. Inner part of megaspore wall. The spore lumen is to the lower right of the micrograph. ×11,250.



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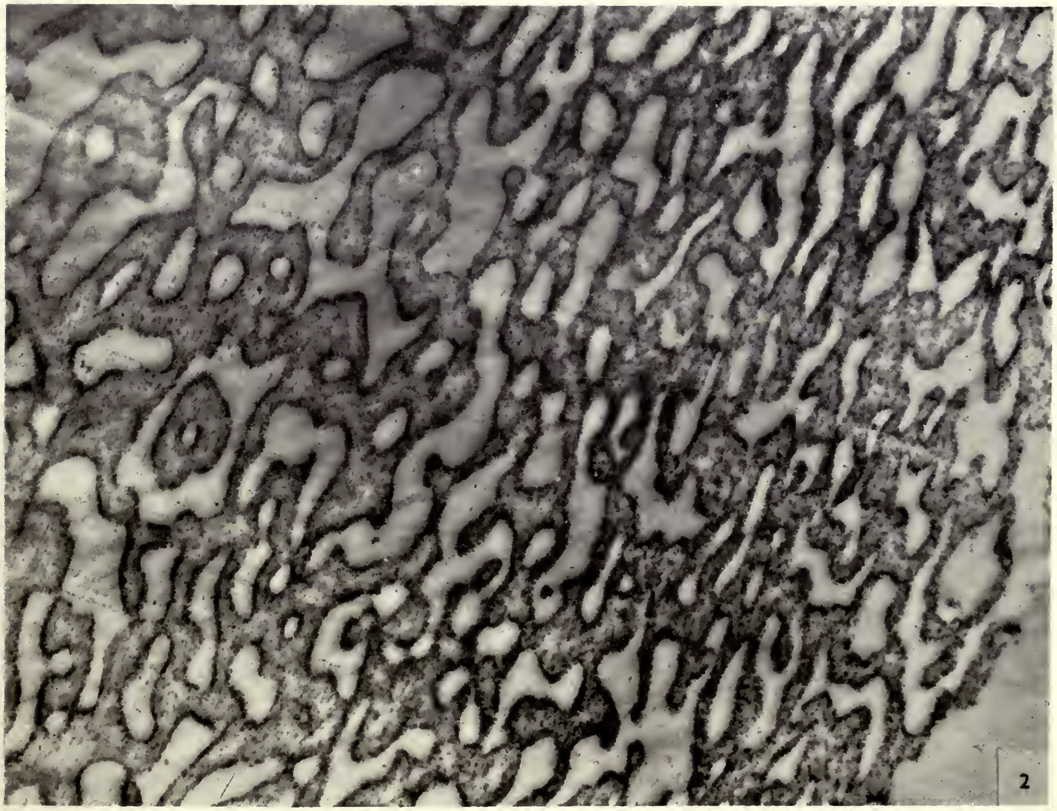

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PLATE 5

Selaginella pulcherrima Liebm. p. 227

FIG. 1. Section of an acetolyzed megaspore wall showing structure of ektexine. The endexine is present as a thin, phase-white layer. Anoptral contrast. × 1,000.

FIGS. 2, 3. Sections of megaspores treated with mercuric bromophenol blue. The spore protoplast in Fig. 2 and the mesospore in Fig. 3 are coloured blue-green. Fig. 2, × 100. Fig. 3, × 128.

FIG. 4. Acetolyzed megaspore containing a mesospore. × 100.

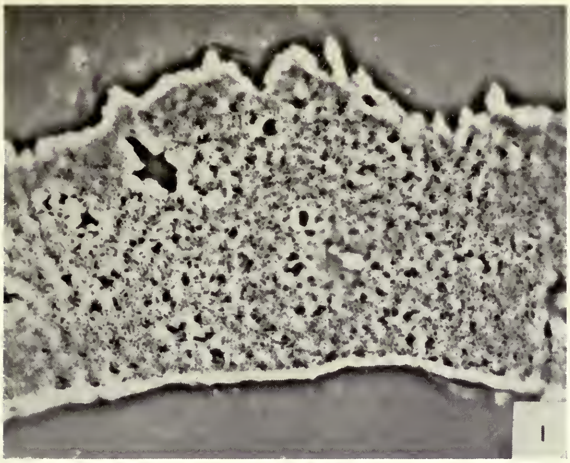
FIG. 5. Tangential section through proximal region of megaspore. The endexine lines the triradiate commissures. × 125. Stained with Bismark brown.

FIG. 6. Section of microspore wall. × 7,500.

Isoetes humilior F. Müll. p. 232

FIG. 7. Section of acetolyzed megaspore wall. Anoptral contrast, × 1,000.

FIG. 8. Section of acetolyzed megaspore wall showing separation of inner part to form a distinct membrane. See also Pl. 6, fig. 1. Anoptral contrast, × 1,000.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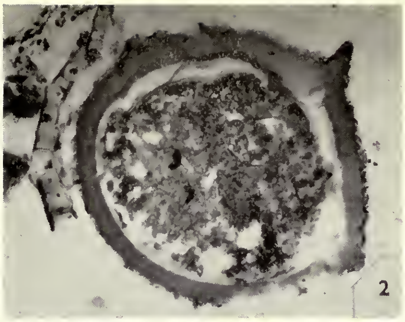
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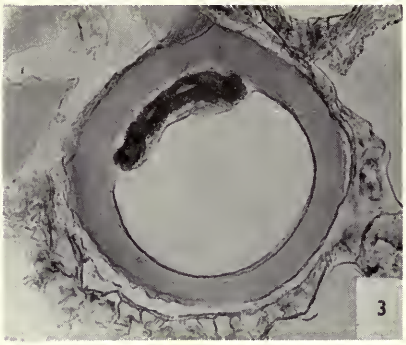
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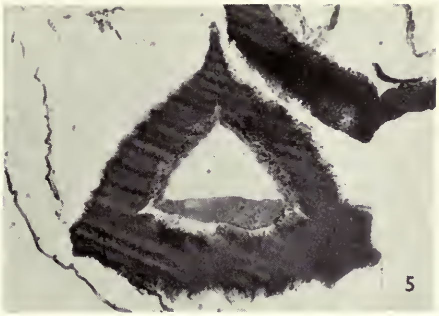
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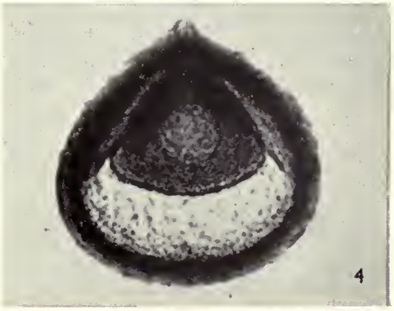
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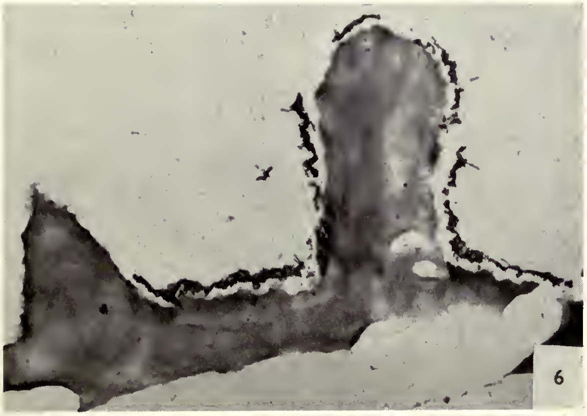
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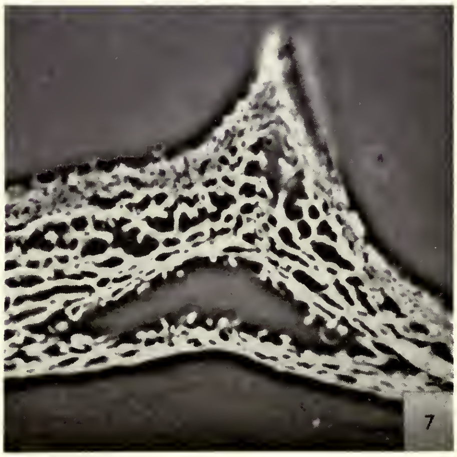
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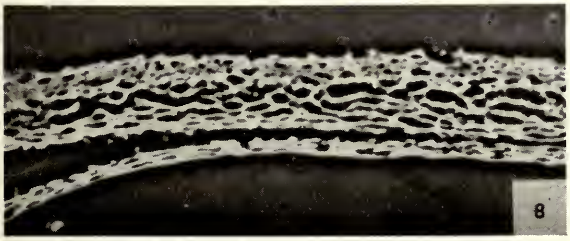
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PLATE 6

Isoetes humilior F. Müll. p. 232

FIG. 1. Section of acetolyzed megaspore showing partial separation of inner part of wall. Anoptral contrast, × 106.

Isoetes echinospora Dur. p. 234

FIG. 2. Section of acetolyzed microspore wall. × 10,000. Section stained with potassium permanganate.

FIG. 3. Section of acetolyzed microspore wall showing separation of inner homogeneous layer from outer lamellated layer. × 7,000.

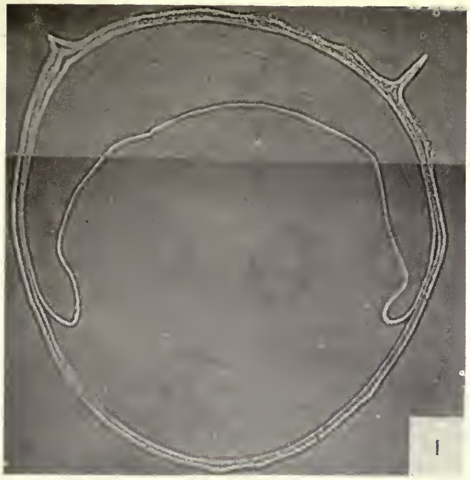
Laevigatisporites cf. ***glabratus*** (Zerndt) p. 235

FIG. 4. Entire megaspore from Lawrence Shale, Kansas. × 20.

FIG. 5. Section of wall. Phase contrast, × 640.

Botrychium jenmanii Underw. p. 254

FIG. 6. Acetolyzed spores showing separation of wall layers. See also Pl. 7, fig. 9. × 370.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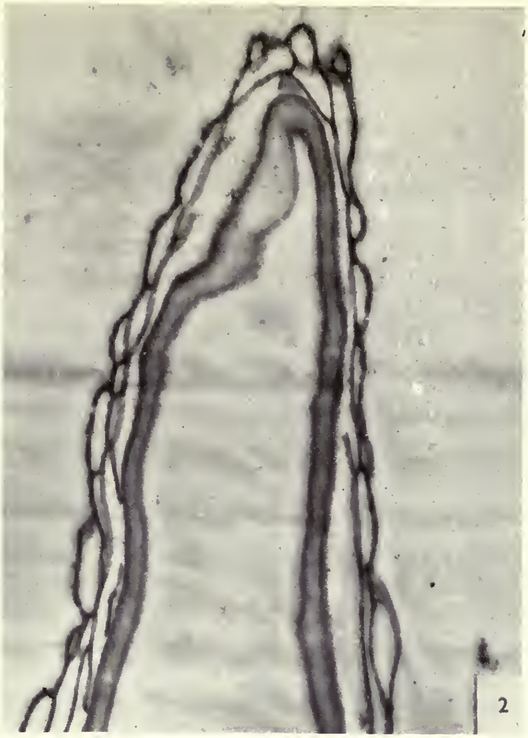
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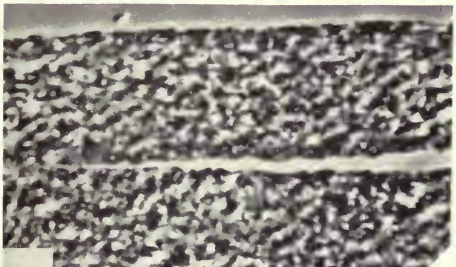
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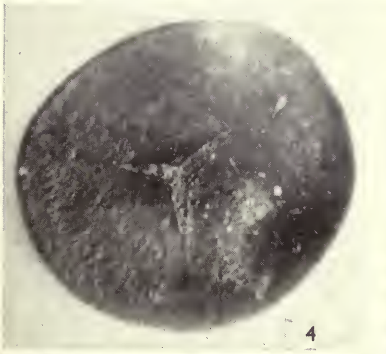
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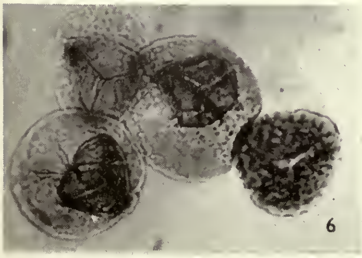
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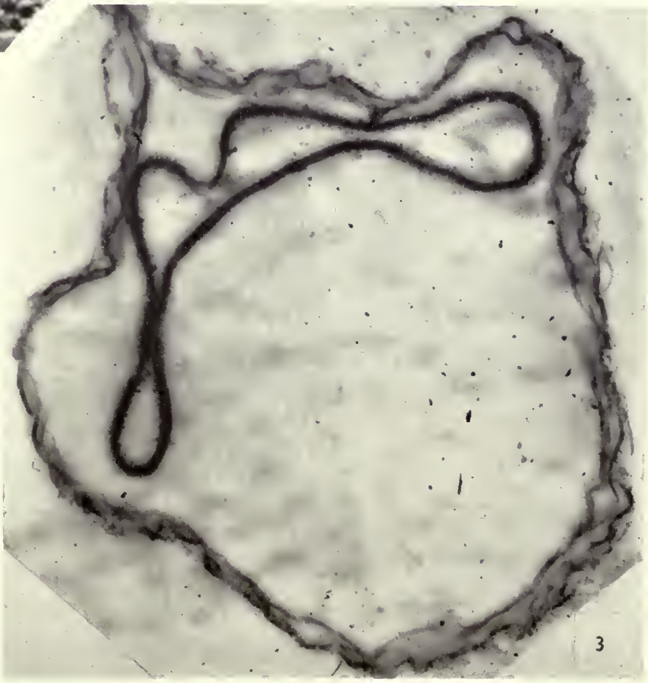
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PLATE 7

Isoetes echinospora Dur. p. 234

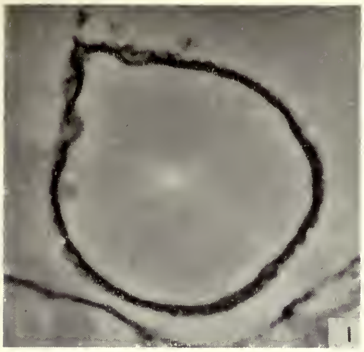
FIGS. 1–8. Acetolyzed microspores showing (except in Fig. 1) separation of wall layers. Figs. 1, 2, 5, 6, 8 sections under phase contrast. Figs. 3, 4, 7 entire spores. For full explanation see text. Fig. 1. ×2,200; Figs. 2, 4. ×1,700; Fig. 3, ×1,500; Fig. 5. ×2,100; Fig. 6, ×1,900; Fig. 7. ×1,000; Fig. 8. ×1,850.

Botrychium jenmanii Underw. p. 254

FIG. 9. Section of acetolyzed spore showing separation of wall layers. See also Pl. 6, fig. 6. Phase contrast, ×925.

Laevigatisporites cf. ***glabratus*** (Zerndt) p. 235

FIG. 10. Section of wall. ×30,000.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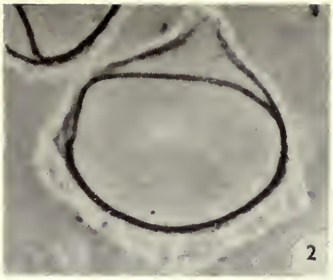
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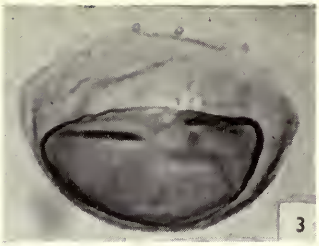
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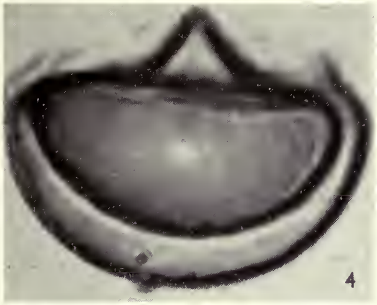
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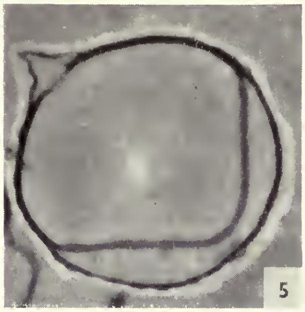
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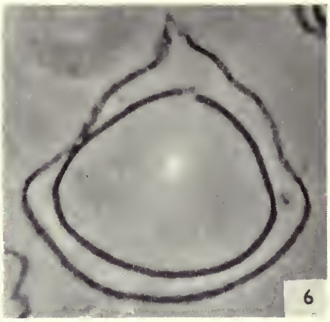
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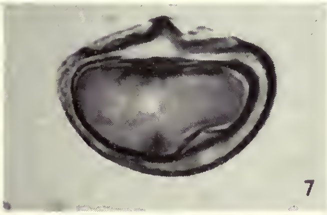
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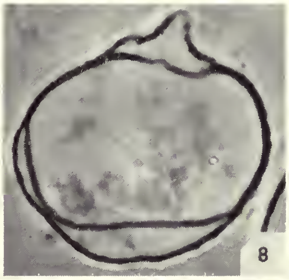
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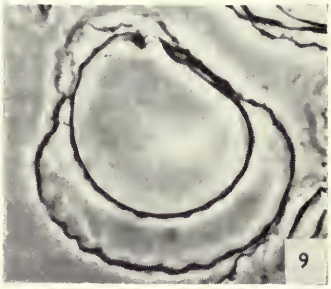
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10

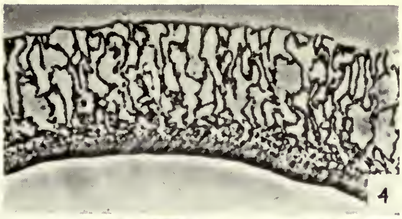
PLATE 8

Marsilea drummondii A. Br. p. 235

Fig. 1. Entire, acetolyzed megaspore. × 42.
Fig. 4. Section of acetolyzed megaspore wall. Phase contrast, × 460.

Marsilea quadrifolia L. p. 235

Figs. 2, 3. Sections of acetolyzed megaspore wall. Fig. 2 is the inner part and Fig. 3 the outer. Both micrographs × 10,000. Sections stained with potassium permanganate.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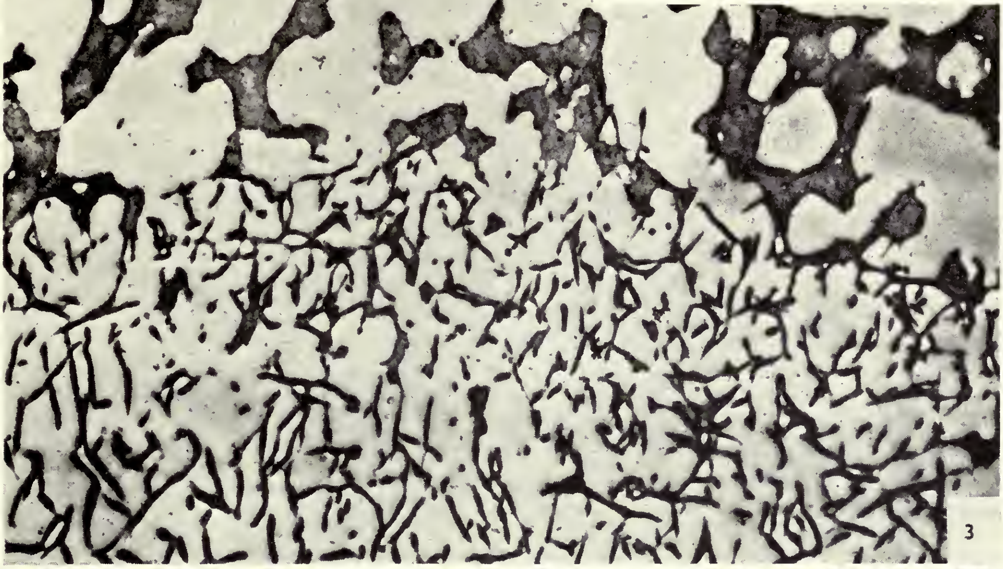
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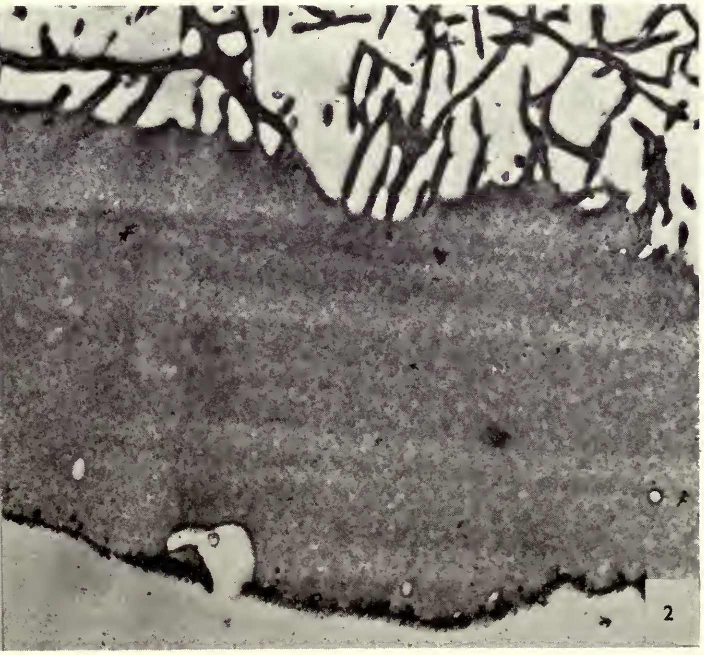
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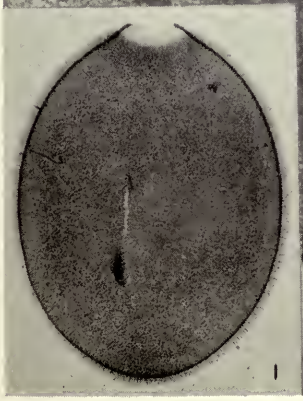
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PLATE 9

Marsilea quadrifolia L. p. 235, 237

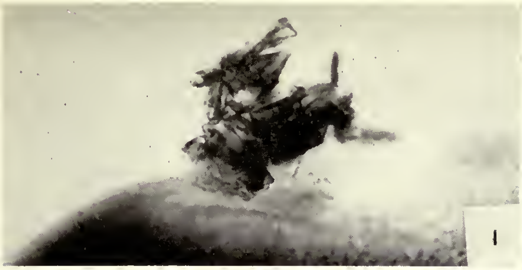
FIG. 1. Apex of acetolyzed megaspore showing abortive spores. ×310.

FIGS. 4, 5. Sections of acetolyzed microspore walls. Fig. 4, ×15,000. Fig. 5, ×12,500. Sections stained with potassium permanganate.

Marsilea drummondii A. Br. p. 235, 237

FIG. 2. Section through apex of acetolyzed megaspore showing structure of abortive spores. Anoptral contrast, ×470.

FIG. 3. Section of acetolyzed microspore wall. ×7,500.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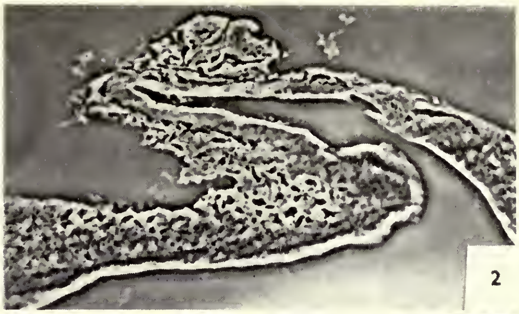
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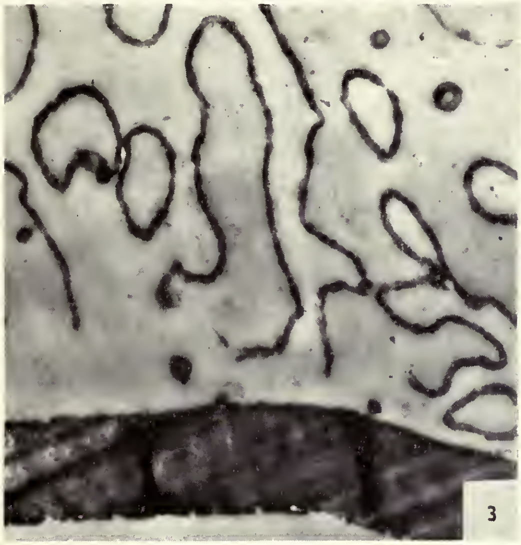
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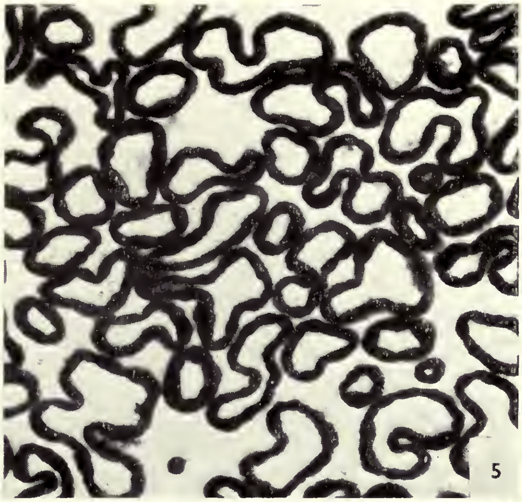
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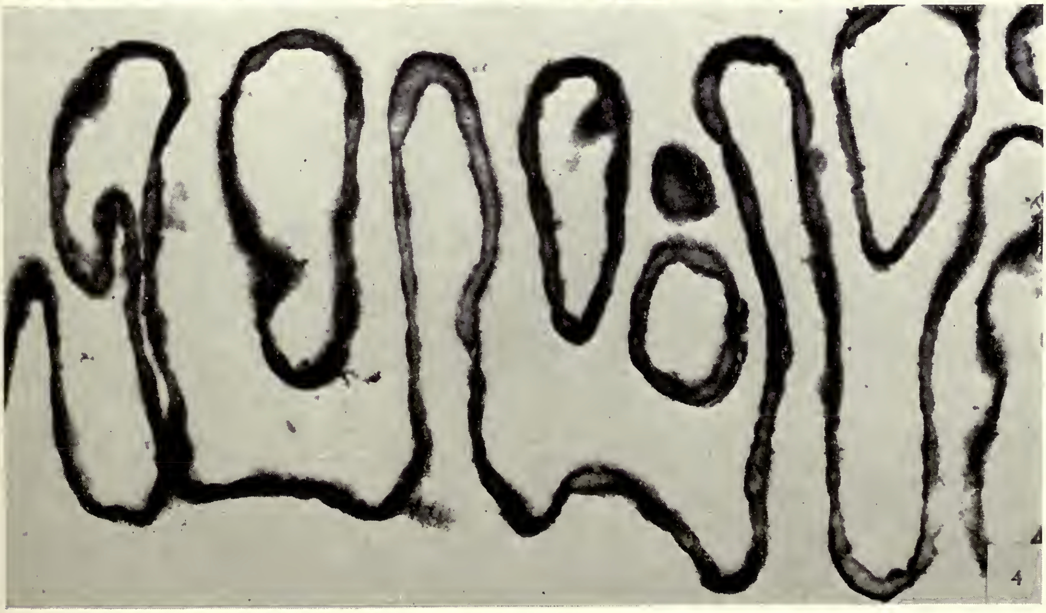
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PLATE 10

Marsilea drummondii A. Br. p. 237

FIG. 1. Mass of normal and abortive spores from acetolyzed microsporangium. × 103.
FIG. 2. Acetolyzed microspore. × 333.

Marsilea quadrifolia L. p. 237

FIGS. 3–8. Sections of acetolyzed microspores showing variation in development of inner wall layer. For full explanation see text. All are anoptral contrast pictures. Fig. 3. × 520; Fig. 4. × 800; Fig. 5. × 880; Fig. 6. × 590; Fig. 7. × 500; Fig. 8. × 600.

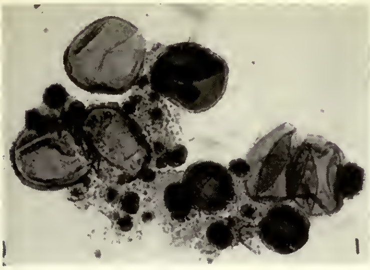
Regnellidium diphyllum Lindm. p. 240

FIGS. 9, 10. Sections of acetolyzed megaspore wall. Phase contrast. Fig. 9. × 660; Fig. 10. × 1,300.

Lycopodium selago L. p. 241

FIG. 11. Section of acetolyzed spore wall. × 5,000.

PLATE 10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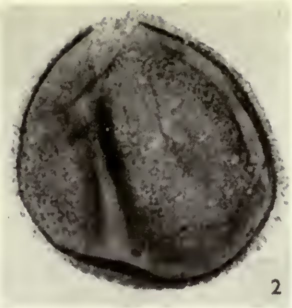
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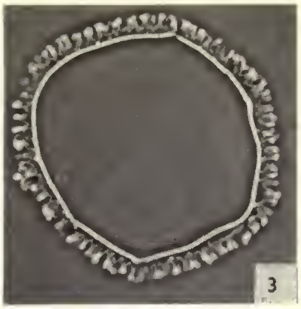
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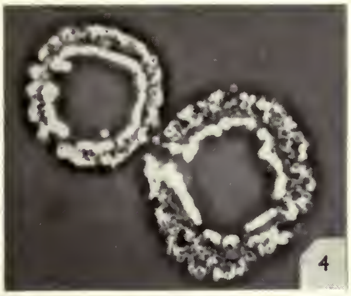
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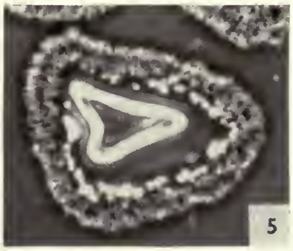
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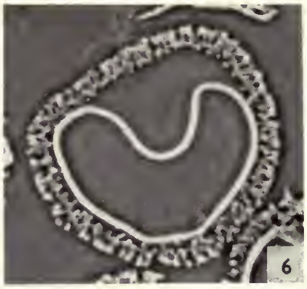
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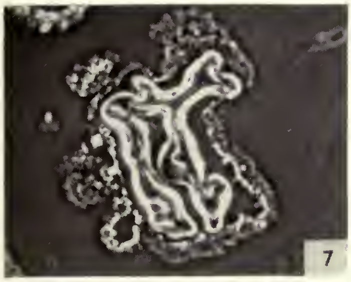
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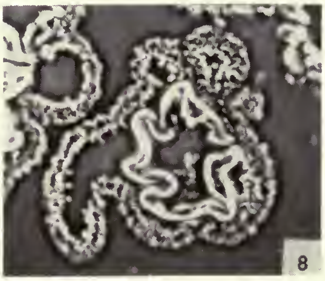
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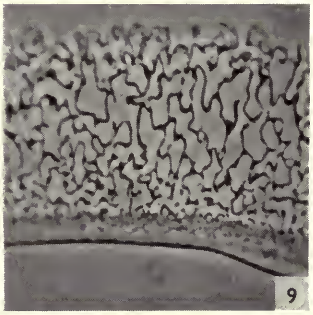
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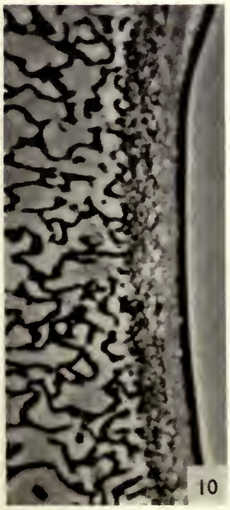
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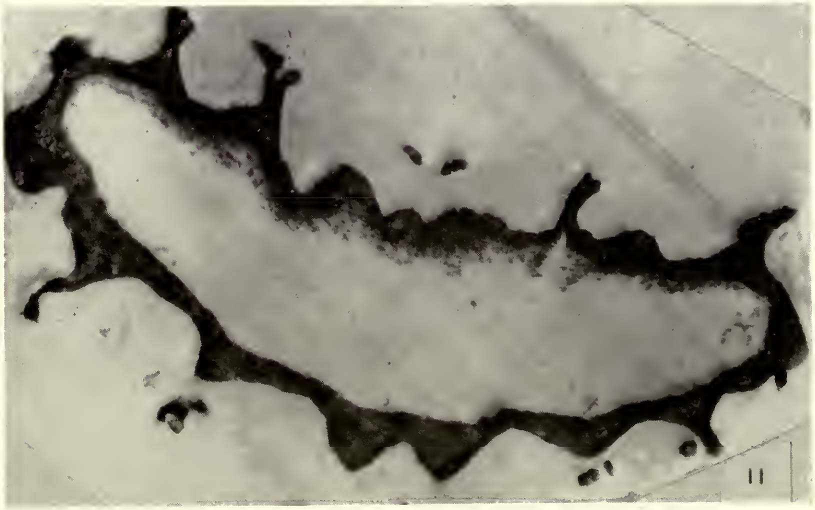
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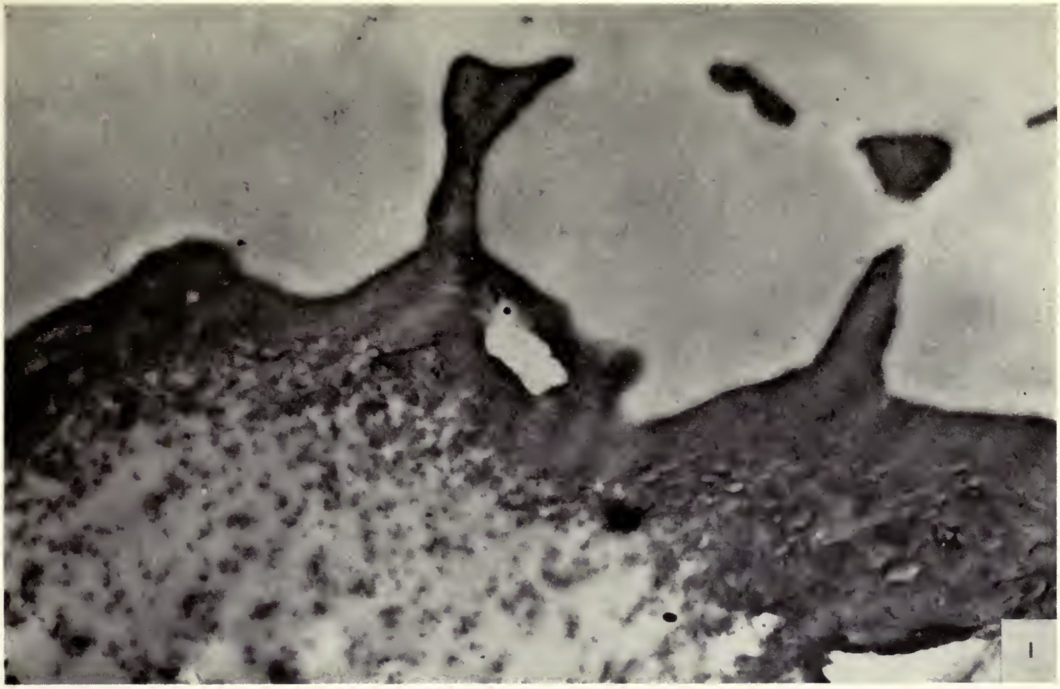
PLATE 11

Lycopodium selago L. p. 241

FIG. 1. Section of acetolyzed spore wall. ×30,000.

Psilotum nudum Griseb. p. 242

FIG. 2. Entire, acetolyzed spore. ×440.
FIG. 3. Section of acetolyzed spore wall. ×10,000. (Section stained with lead hydroxide.)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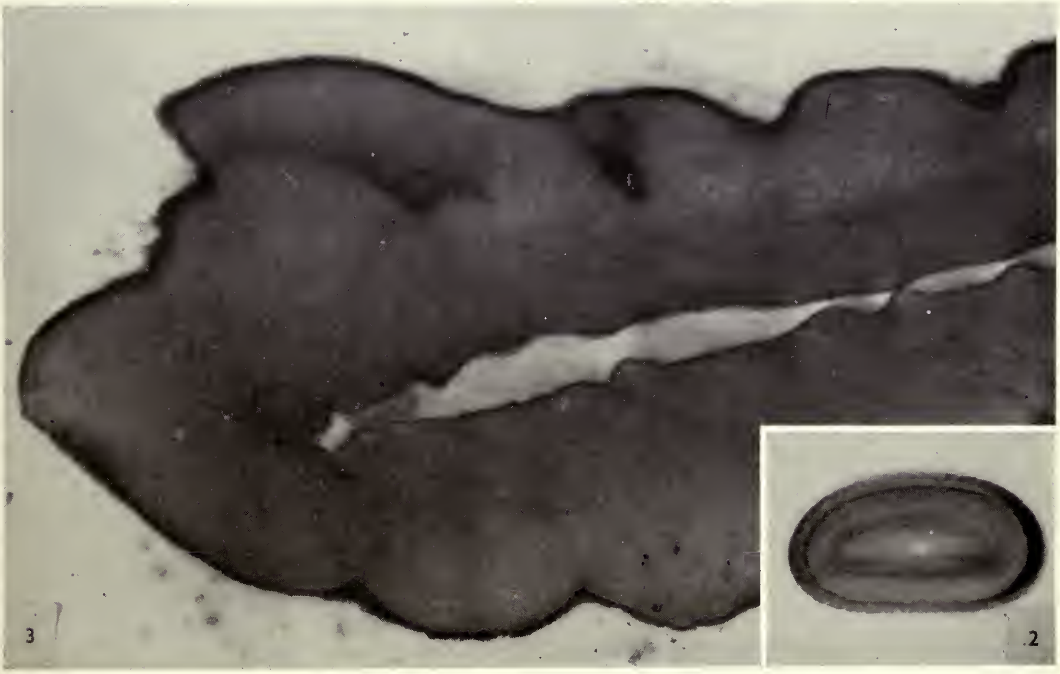
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PLATE 12

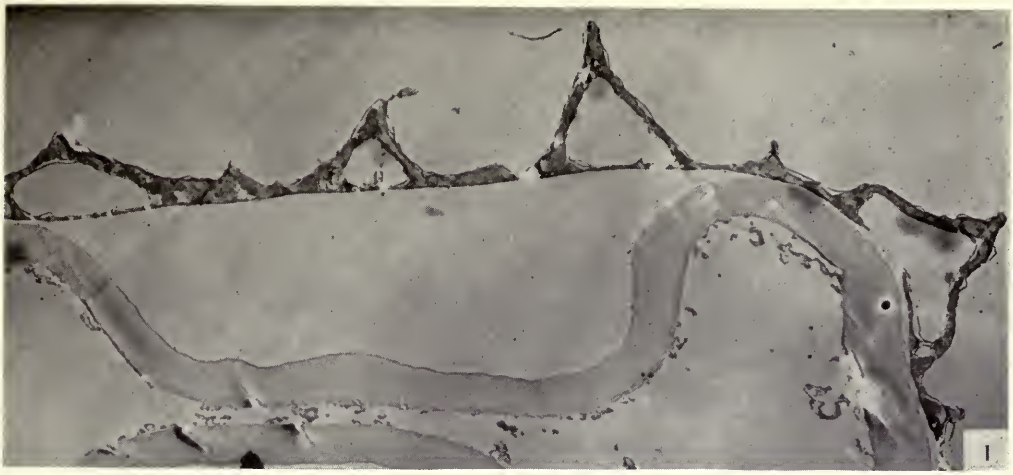
Asplenium adiantum—nigrum L. p. 242

FIGS. 1, 2. Sections of acetolyzed spore walls. Fig. 1, × 3,000. Fig. 2, × 12,500.
FIG. 5. Entire, acetolyzed spore. × 770.

Archaeotriletes sp. p. 243

FIGS. 3, 4. Sections of wall. Fig. 3, × 10,000. Fig. 4, × 6,250.

PLATE 12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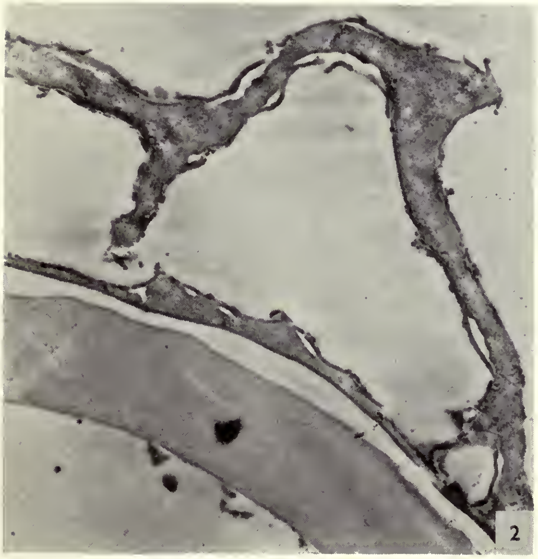
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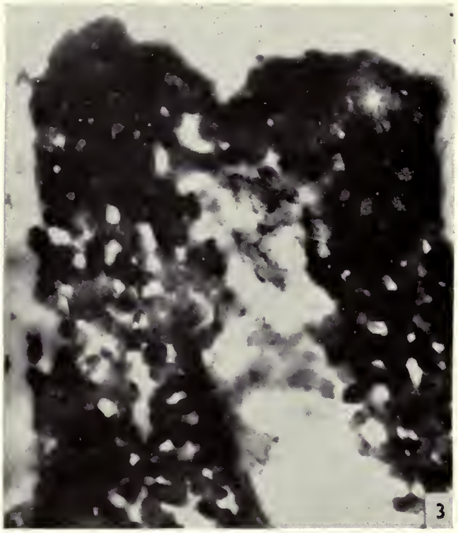
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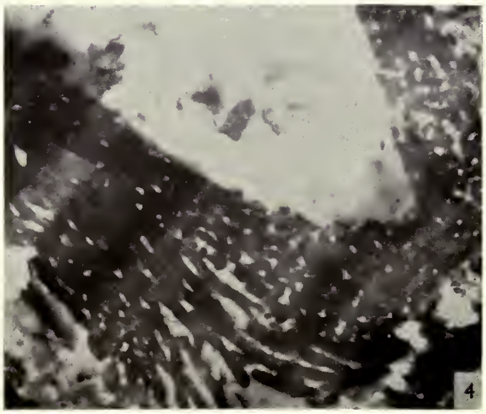
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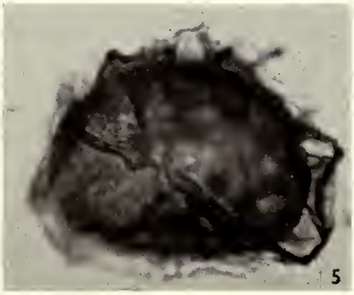
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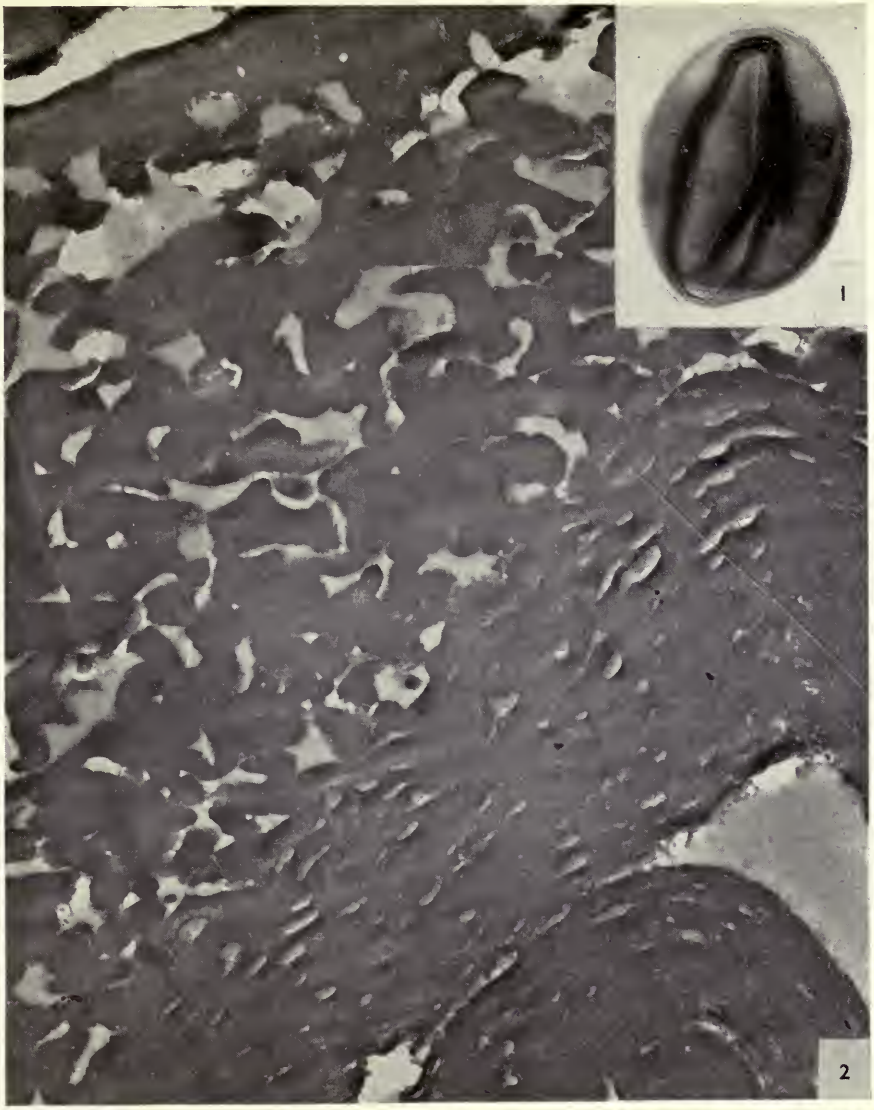
PLATE 13

Schopfipollenites sp. p. 243

FIG. 1. Entire grain from Lawrence Shale, Kansas. ×200.

FIGS. 2, 3. Sections of wall. The outer edge of the grain is at the top left of fig. 2, the lumen is at the bottom right. Fig. 2, ×22,500. Fig. 3, ×4,000.



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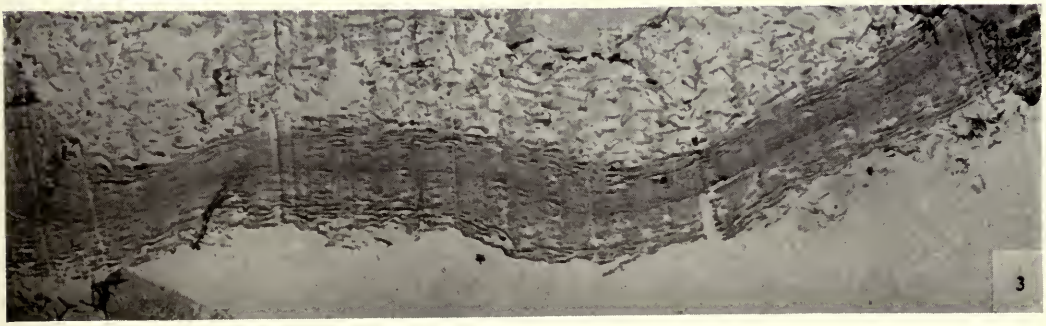

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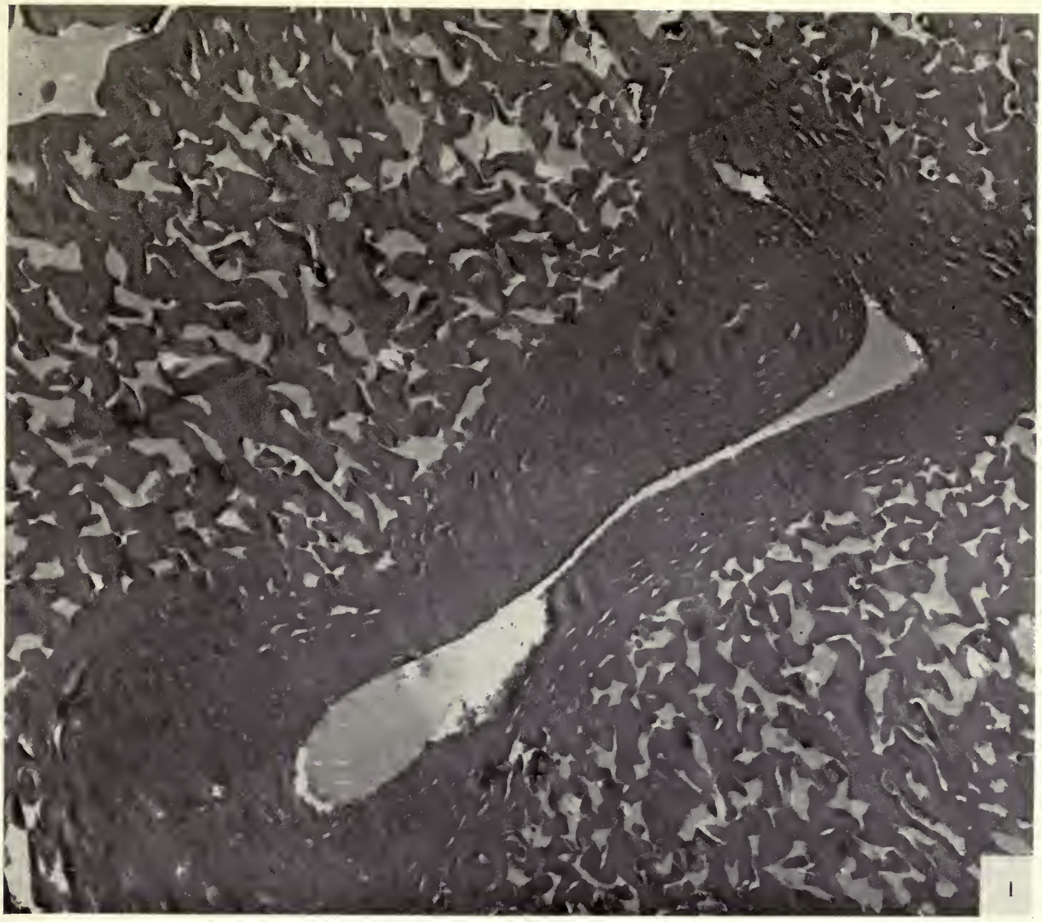
PLATE 14

Schopfipollenites sp. p. 243

FIG. 1. Sections of the wall. × 10,000.

Encephalartos villosus Lem. p. 244

FIG. 2. Section of acetolyzed pollen wall. × 10,000.



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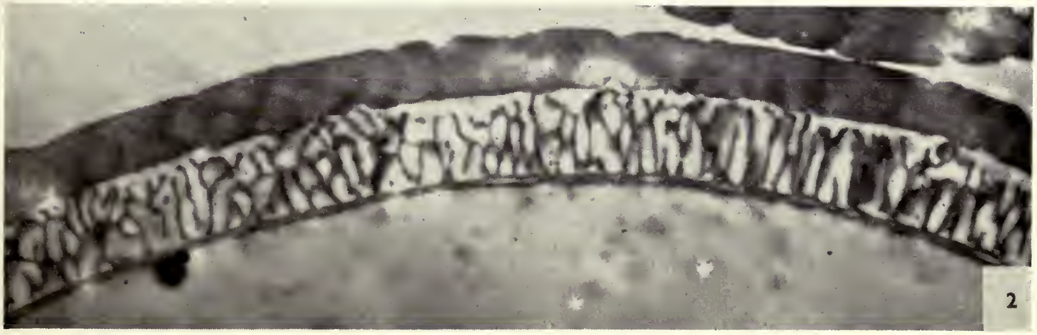


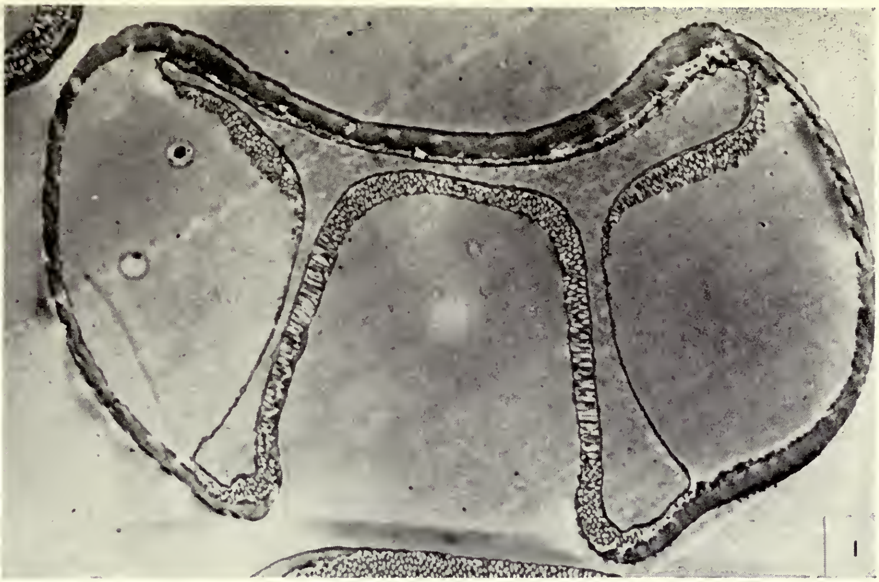
2

PLATE 15

Encephalartos villosus Lem. p. 244

FIGS. 1, 2. Sections of acetolyzed pollen walls. Fig. 1 is more or less transverse and Fig. 2 more or less longitudinal. Both micrographs × c. 2,500.

FIG. 3. Entire, acetolyzed pollen grain. × 1,600.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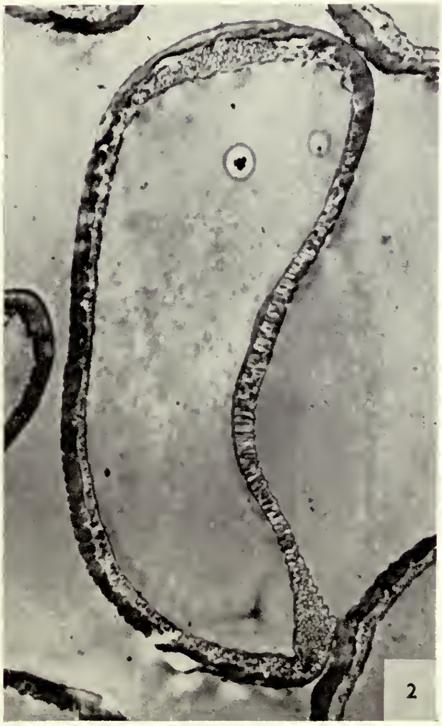
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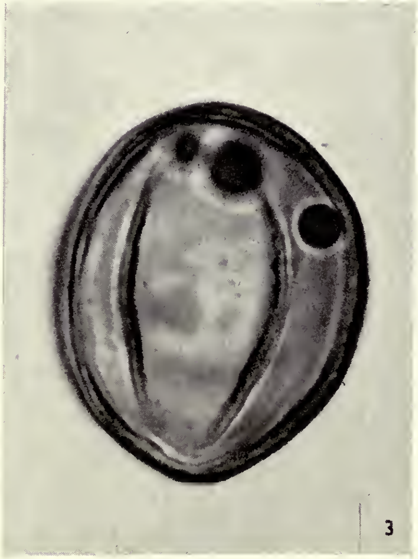
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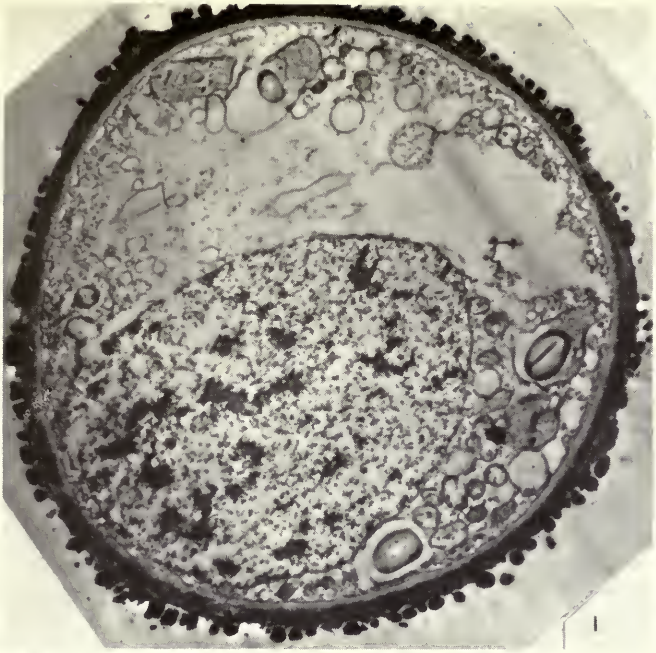
PLATE 16

Taxus baccata L. p. 245

FIGS. 1–3. Sections of pollen grains fixed in glutaraldehyde and post-fixed in osmium tetroxide. Fig. 1, ×c. 6,000. Fig. 2, ×20,000. Fig. 3, ×15,000.

FIG. 4. Micrograph showing small, electron-dense droplets in tapetal cell cytoplasm. (Fixed in glutaraldehyde, post-fixed in osmium tetroxide.) ×15,000.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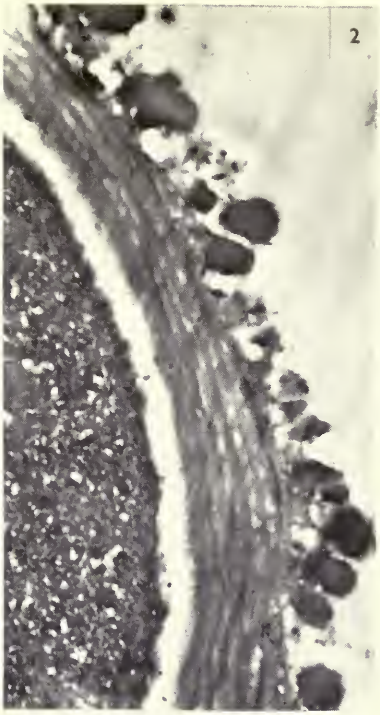
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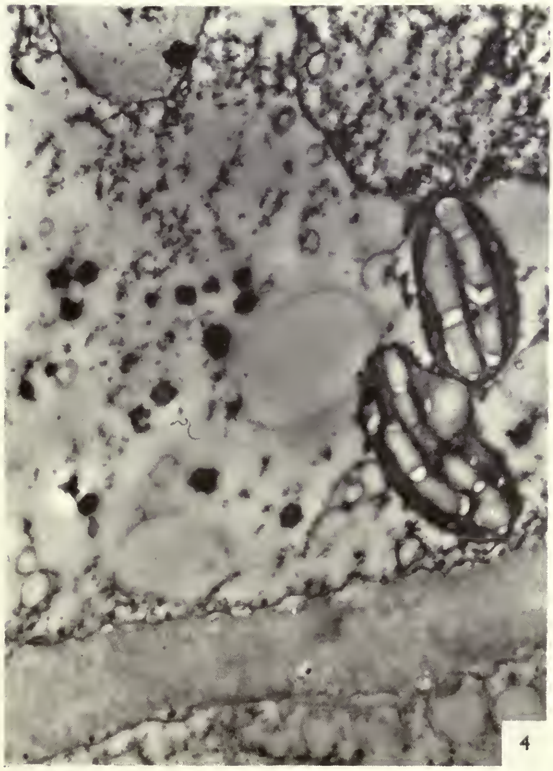
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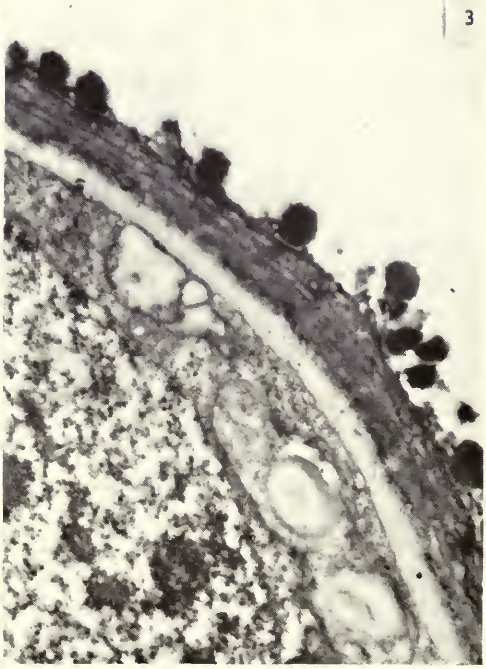
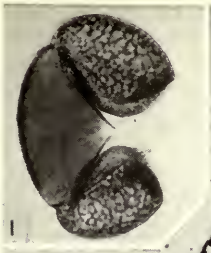

3

PLATE 17

***Pinus sylvestris* L.** p. 246

FIG. 1. Entire, acetolyzed pollen grain. ×280.

FIGS. 2–4. Sections of pollen grains fixed in glutaraldehyde and post-fixed in osmium tetroxide. Fig. 4 shows the " foot layer " forming the floor of the saccus and the underlying endexine. Fig. 2, × c. 2,000. Fig. 3, ×7,500. Fig. 4, ×30,000.



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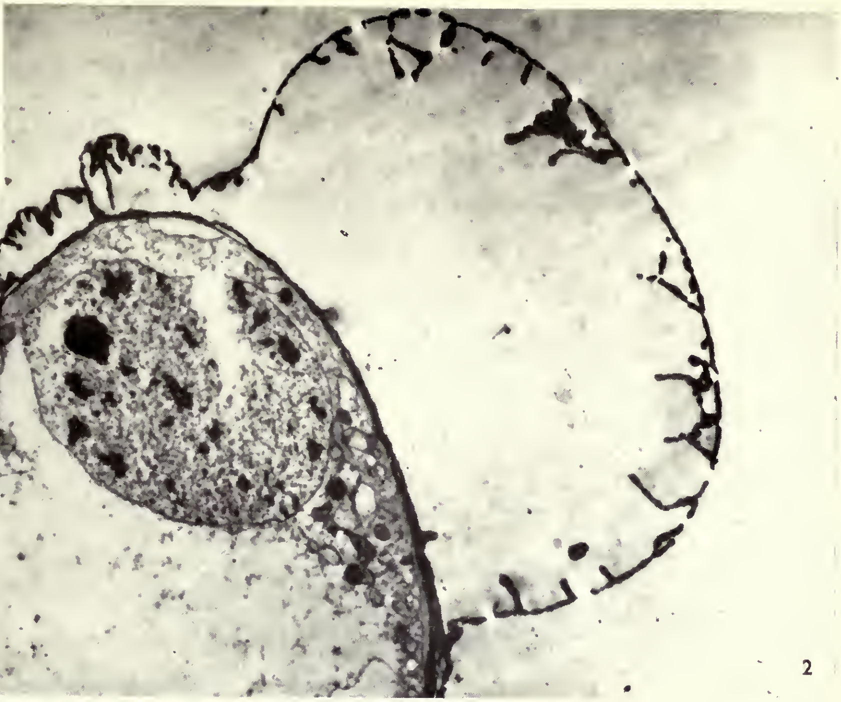

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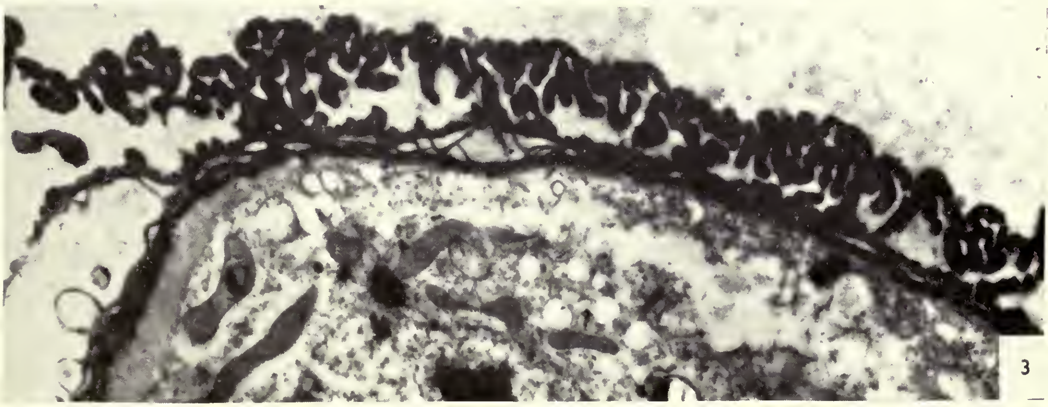

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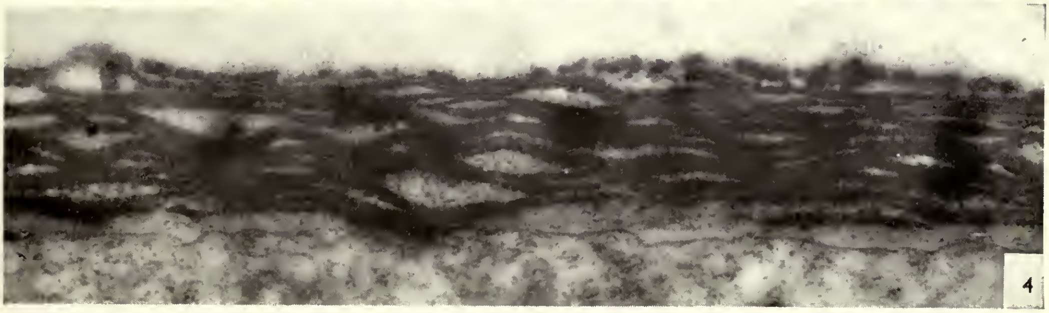

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PLATE 18

Pinus sylvestris L. p. 246

Fig. 1. Section of pollen grain showing origin of a saccus. (Fixed in glutaraldehyde and post-fixed in osmium tetroxide.) × 10,000.

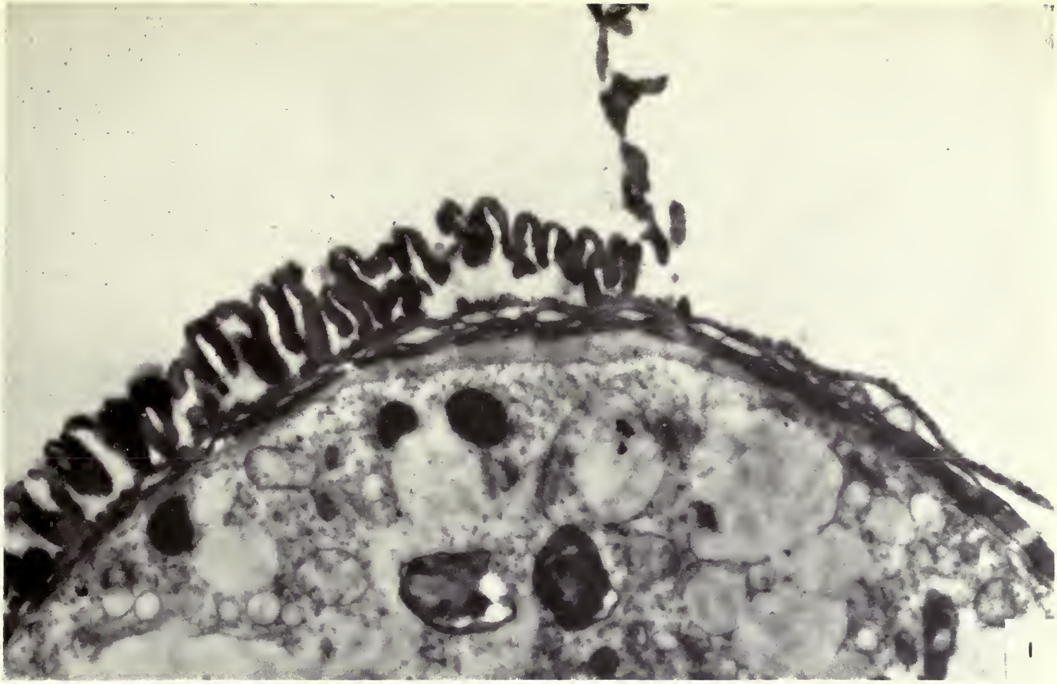
Fig. 2. Micrograph showing the Ubisch body-like objects adjacent to tapetal cell wall. Part of saccus of pollen grain forms an arc in lower part of figure. (Fixed in glutaraldehyde and post-fixed in osmium tetroxide.) × 7,500.

Trigonocarpus sp. p. 247

Fig. 3. Section of megaspore membrane. Anoptral contrast, × 570.

Taxospermum undulatum Neely p. 247

Fig. 4. Surface view of megaspore membrane. Phase contrast, × c. 600.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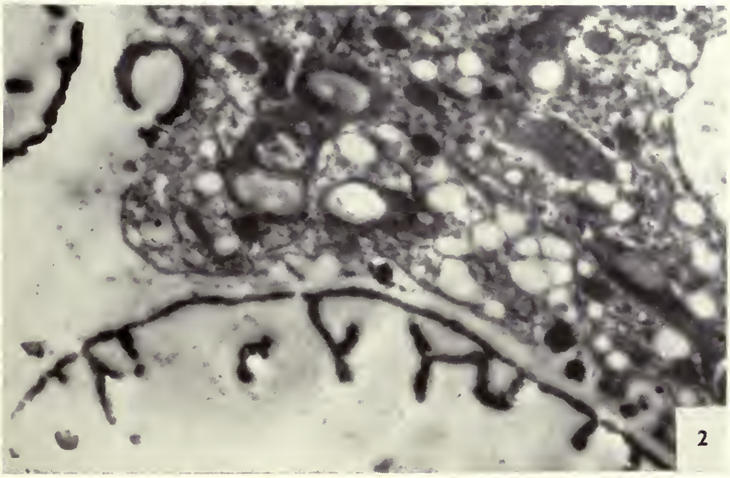
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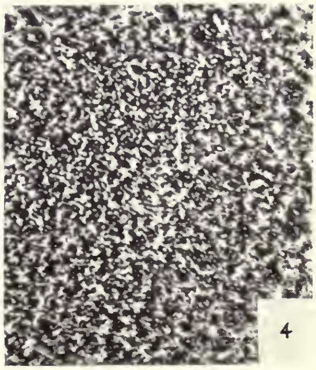
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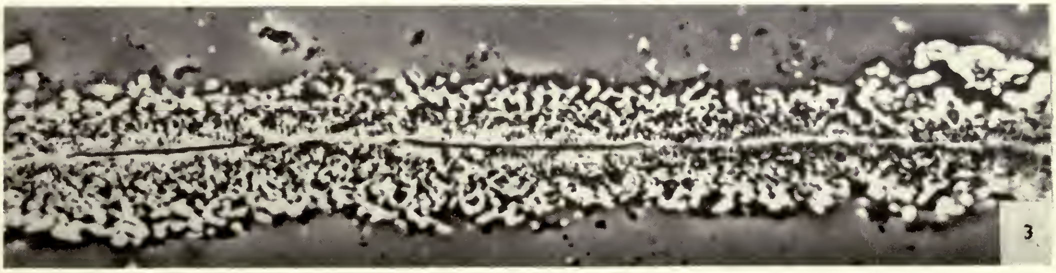
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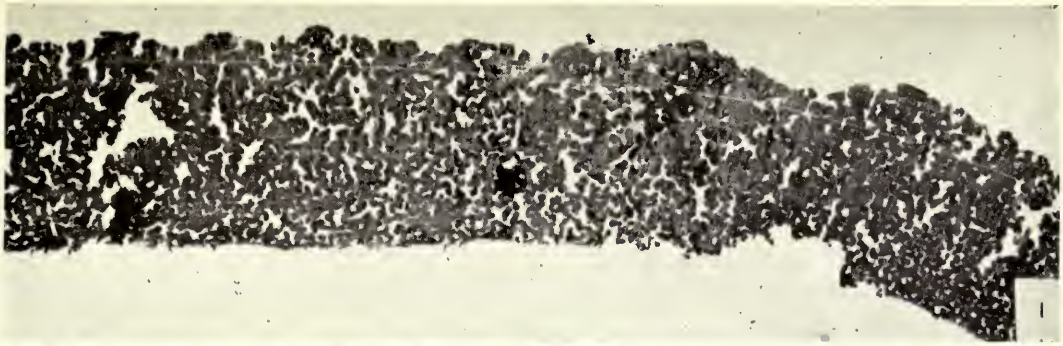
PLATE 19

FIGS. 1–3. Sections of megaspore membrane from cordaite ovule. Fig. 3 shows the inner edge of the membrane. Fig. 1, × c. 2,000. Fig. 2, ×30,000. Fig. 3, ×6,250.

Florinites sp. p. 253

FIG. 4. A mass of pollen grains from Lawrence Shale, Kansas. ×500.

FIG. 5. Section of pollen wall. The inner, granular layer is towards the bottom of the micrograph. ×10,000.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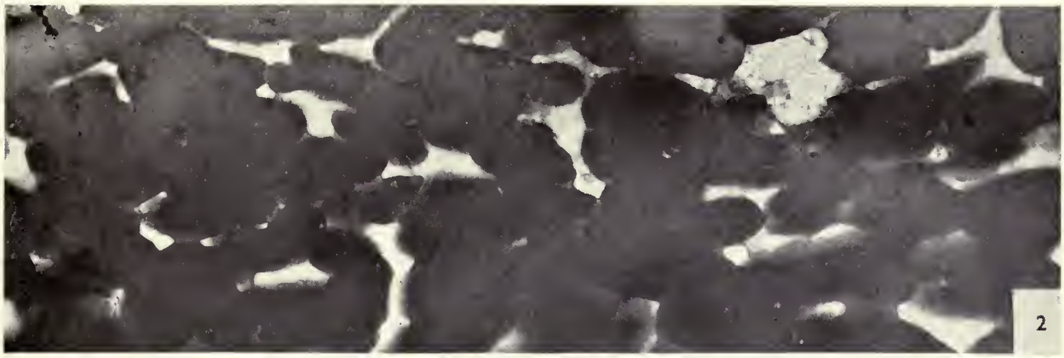
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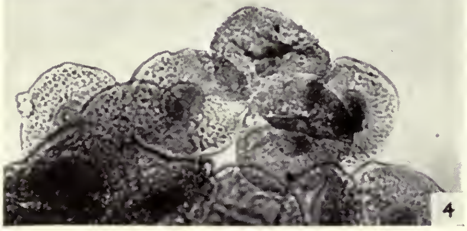
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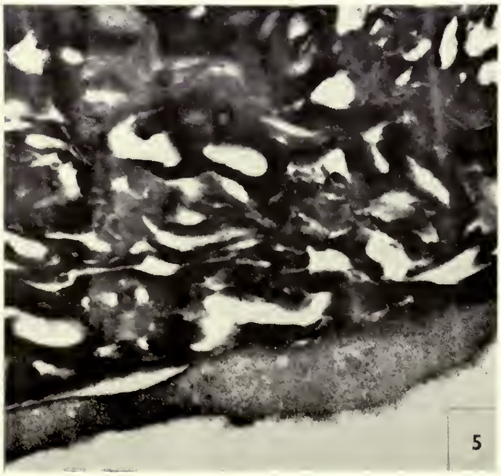
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PLATE 20

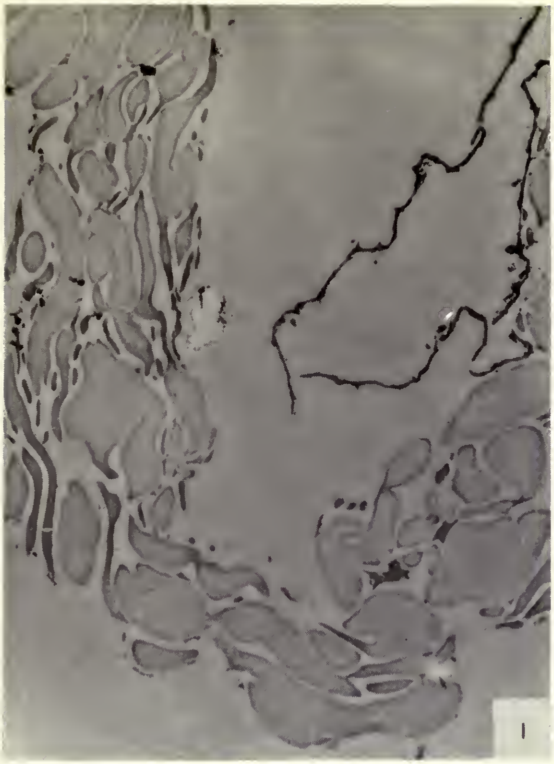
Cystosporites giganteus (Zerndt) p. 248

FIGS. 1, 2. Sections of wall of large, presumably fertile megaspore. Fig. 1, × c. 1,500. Fig. 2m × c.1,800.

Dicranum scoparium Hedw. p. 250

FIG. 3. Section of acetolyzed spore. × 10,000.

FIG. 4. Section of part of acetolyzed capsule showing electron-dense droplets concentrated in zone adjacent to remnants of capsule wall and randomly distributed between spores. × c. 2,000. Section stained with potassium permanganate.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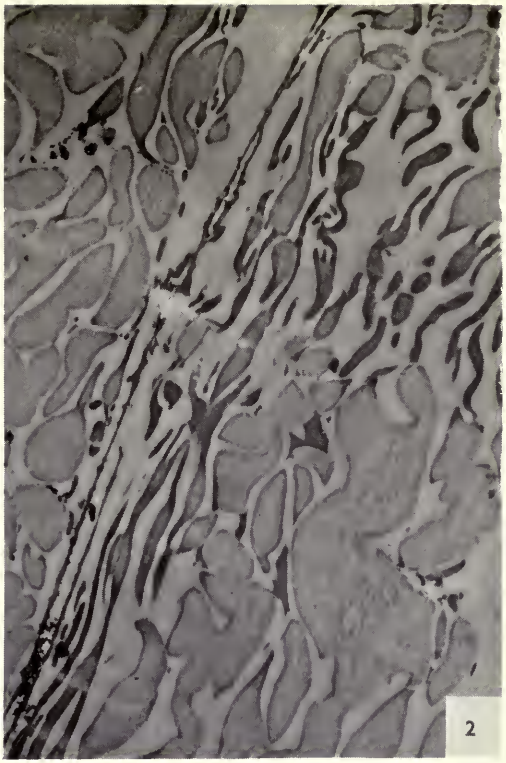
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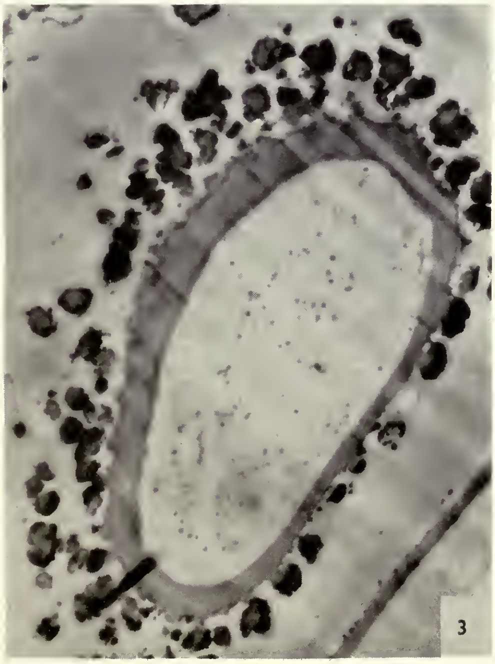
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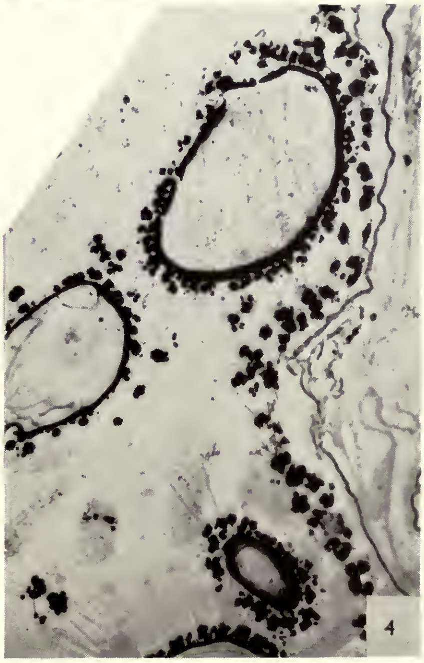
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PLATE 21

Didymosporites scotti Chaloner p. 249

FIGS. 1–3. Sections of wall of large, presumably fertile megaspores. Fig. 1 is an electron micrograph, Figs. 2, 3 are anoptral contrast pictures. Fig. 1, × 11,250. Figs. 2, 3, × 1,600.

FIG. 4. Complete tetrad from the Lower Carboniferous of Fife, Scotland. Abortive spores can be seen on left of figure between two large, presumably fertile spores. × 120.

Salvinia auriculata Aubl. p. 251

FIG. 5. Mass of resistant material containing microspores released from an acetolyzed microsporangium. × 254.

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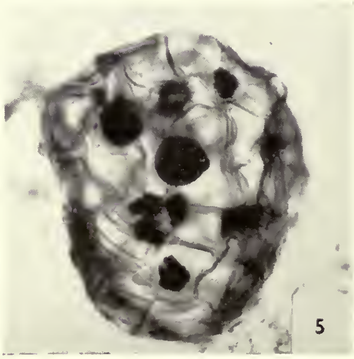
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NEW GYMNOSPERMS FROM THE TICÓ FLORA, SANTA CRUZ PROVINCE, ARGENTINA

S. ARCHANGELSKY

BULLETIN OF
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GEOLOGY Vol. 13 No. 5
LONDON : 1966

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NEW GYMNOSPERMS FROM THE TICÓ FLORA, SANTA CRUZ PROVINCE, ARGENTINA

BY

SERGIO ARCHANGELSKY
Museo de Ciencias Naturales, La Plata
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Xuf.

Pp. 259–295 ; 8 *Plates* ; 39 *Text-figures*

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NEW GYMNOSPERMS FROM THE TICÓ FLORA, SANTA CRUZ PROVINCE, ARGENTINA

BY

By SERGIO ARCHANGELSKY

SYNOPSIS

The Lower Cretaceous plants described here were collected between 1958 and 1963 from different localities on the outcrop of the Baqueró Formation. A new locality, Bajo Grande, yielded good mummified plant fragments. Two new genera, *Trisacocladus* and *Apterocladus* are described and referred to the family Podocarpaceae. *Trisacocladus tigrensis* gen. et sp. nov. from Bajo Tigre is based on leafy shoots with male cones attached, as well as on female structures probably also connected organically to leafy branches. The male cones yielded 3-saccate pollen grains of the type usually referred to *Trisaccites*. *Apterocladus lanceolatus* gen. et sp. nov., from Bajo Grande, is also based on leafy shoots with attached male cones possessing pollen grains with three rudimentary air bladders. The following new species of fern-like cutinized fronds are described : *Pachypteris elegans*, *Almargemia incrassata* and *Ticoa lamellata* ; together with the conifers *Podocarpus dubius*, *Tomaxellia biforme*, and two new species of *Araucarites* (*A. minimus* and *A. baqueroensis*) both of which are based on ovuliferous scales.

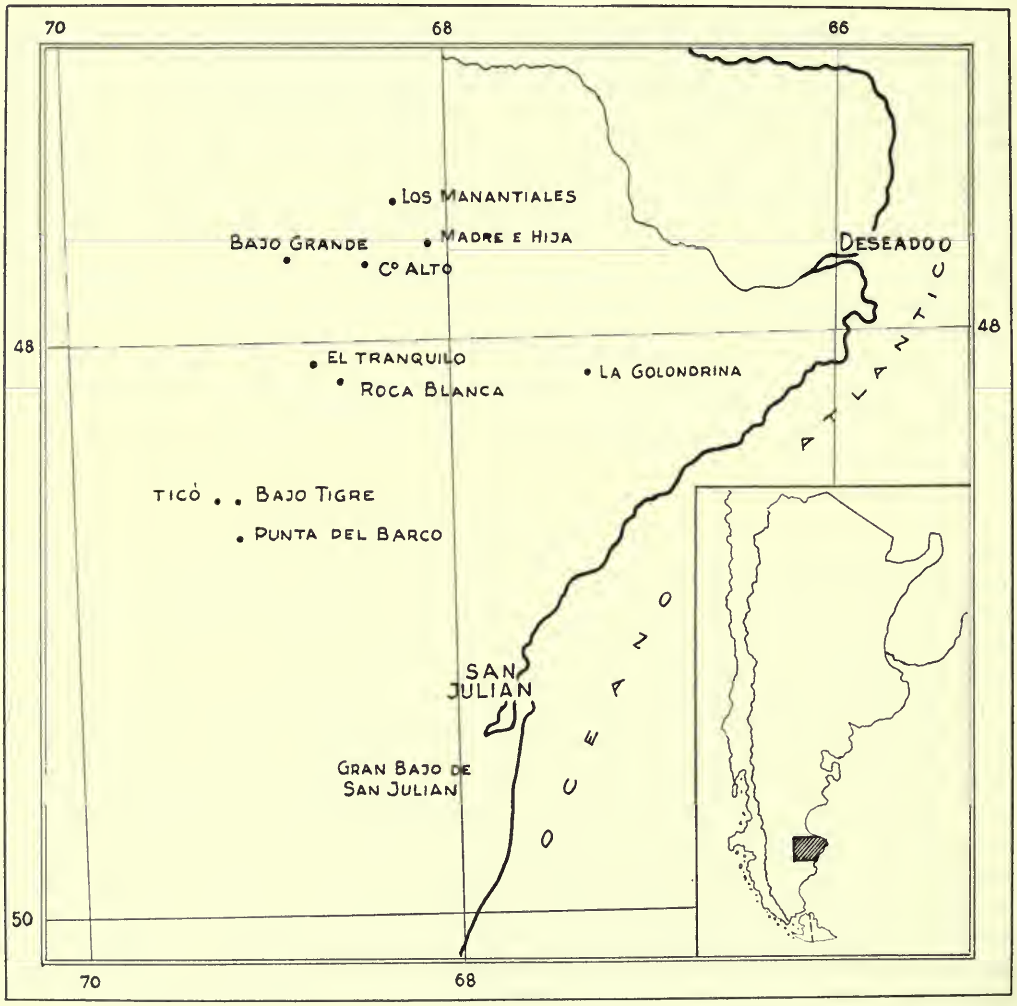
The original diagnosis of *Tomaxellia degiustoi* is revised in the light of new and better preserved material from the type localty (Ticó Amphitheatre). The description of these taxa adds considerably to the Lower Cretaceous flora of Patagonia which presently contains about 70 species, many with cuticular structure preserved.

I. INTRODUCTION

THE fossil plants described in the present paper were collected in the Ticó Amphitheatre, Bajo Tigre and Bajo Grande of Santa Cruz Province (Southern Argentina), during the years 1958–63. References to the Ticó and Bajo Tigre localities have already been made (Archangelsky 1963, 1965). The new locality, Bajo Grande, has been mentioned but without descriptions of its fossil plants.

The Baqueró Formation in Bajo Grande constitutes most of the " cliffs " (*barranca* in Spanish) which surround a large geographic depression (*bajo* in Spanish). In Bajo Grande, as in most localities, this formation is composed of nearly horizontal strata which cover sediments referred to the Matilde Formation of Middle to Upper Jurassic age. Bajo Grande is the third locality which has yielded mummified plant fragments ; the sediments being more indurated yielded a large variety of species. In Ticó and Bajo Tigre, the plants occur in lenticular beds at different levels in the sections. Each bed usually contains a few species only, but these are represented by many specimens, some of which are dominant in the association. The plants in Bajo Grande are usually more fragmentary and may have drifted for a longer distance before deposition. The only bed so far discovered in Bajo Grande has been named the *Araucarites* bed, because ovuliferous scales of this genus are very common, although other taxa are well represented.

The Baqueró Formation in Bajo Grande and elsewhere is divided into an upper and a lower member. The lower member, which includes the mummified plant material, has sediments of a somewhat darker colour and coarser grain (conglomerates, sandstones, etc. of grey, violet and similar colours) and is absent in some areas. The upper member is always white to yellow in colour and consists usually of volcanic ash (tuff). It is geographically widespread and may contain plant impressions or be totally devoid of fossils. The total thickness of the Baqueró Formation in all the areas so far surveyed, seldom exceeds 100 metres.


70
68
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Los Manantiales
Madre e Hija
Bajo Grande
Cº Alto
Deseado
El Tranquilo
Roca Blanca
La Golondrina
Ticó
Bajo Tigre
Punta del Barco
San Julian
Gran Bajo de San Julian
Oceano Atlantico

Map showing the main localities mentioned in the paper. In addition, the following three localities yielding rich floras are included : La Golondrina (Permian), El Tranquilo (Triassic) and Roca Blanca (Liassic).

On the evidence of the rich flora a Lower Cretaceous age is postulated for the Baqueró Formation, and all references to an Upper Cretaceous age should be abandoned. Consequently all correlations with the Upper Cretaceous Chubut Series (especially its Yellow Tuffs Formation or " *Tobas Amarillas* ") are erroneous.

All previously recorded localities and those referred to in the present paper are represented in the map on p. 262.

The fossil plants described are all Gymnosperms. In 1965 references were made to a conifer associated with *Ginkgoites tigrensis*, having male and female cones in organic connection. This material, from Bajo Tigre, is here fully described and referred to the family Podocarpaceae. Good specimens of *Tomaxellia degiustoi* from the type locality in Ticó are also described and add to our knowledge of its gross morphology. The rest of the material described comes from the new Bajo Grande locality. Three species of cutinized fern-like fronds are referred to the genera *Pachypteris*, *Almargemia* and *Ticoa*. Two species of ovuliferous scales are included in the genus *Araucarites* (some material from Bajo Tigre and Ticó is also included in one of the species). Leafy branches with male cones in organic connection are referred to a new genus of the Podocarpaceae, *Apterocladus*, while sterile leafy branches are referred to a new species of *Podocarpus*. Finally a new species of *Tomaxellia* is described. The remaining material from Bajo Grande, which will be described in the near future, includes conifers of *Brachyphyllum* type, isolated male and female cones, Bennettitales and a few fern fragments.

The usual maceration technique (nitric acid followed by alkali) has been followed. Some delicate cuticles were treated only with very dilute alkali. A few transfers were also made.

The material studied belongs to the following collections: La Plata Natural History Museum (LP), Argentina; Lillo Institute of Tucuman (LIL), Argentina and the British Museum (Natural History) (BMNH, V.) Great Britain.

II. SYSTEMATIC DESCRIPTIONS

GYMNOSPERMAE

Abundant fern-like fronds possessing a thick cuticle are present in the Ticó flora. New generic names have been established for these based on cuticular characters (Archangelsky 1963); they were included in the Gymnosperms. The new material described here confirms the importance of these plants which occur in most of the localities where the Ticó flora has been found. In the absence of fructifications the natural relationship of these leaves is uncertain, but their cuticular structure strongly suggests their inclusion in the Pteridospermae and Cycadales. Three new species are described in the present work, *Ticoa lamellata* which resembles some living Cycads in epidermal characters, *Almargemia incrassata* also placed in or near the Cycads, and *Pachypteris elegans* which has characters in common with some Recent members of the Cycadales, although it also has similarities with the Pteridosperms. These leaves being abundant fossils must belong to species important in the Lower Cretaceous vegetation of Patagonia.

Genus ***PACHYPTERIS*** Brongniart 1828

Pachypteris elegans sp. n.

(Pl. 1, fig. 1 ; Pl. 2, figs. 10–12 ; Text-figs. 1–5)

DIAGNOSIS. Leaf bipinnate, oblong, 5 cm. long × 2 cm. wide (base missing). Leaf rachis strong, 2 mm. wide. Pinnae opposite to subopposite, separated by 3–4 mm., lanceolate, up to 13 mm. long × 5 mm. wide, forming an angle of 45–60° with main rachis. Pinna rachis up to 1·5 mm. wide. Pinnules subopposite to alternate, arising at about 45° to pinna rachis, oblong to lanceolate with rounded apex and margins entire, up to 1·5 mm. long × 0·75 mm. wide ; lower margin decurrent and connecting with upper margin of pinnule below. Lower catadromic pinnule often once lobed and seated on the axil of pinna and main rachises. Mid-vein present up to near apex of pinnule, decurrent at base. Few simple lateral veins given off at acute angles. Substance of lamina thick.

Upper and lower cuticles up to 5 μ thick. Upper cuticle without stomata. Cells isodiametric, 25–50 μ, becoming rectangular near margins and on rachis. Anticlinal walls thick, unpitted, up to 5 μ, deeply cutinized. Cell surface finely granular. Lower cuticle with stomata ; shape and size of epidermal cells as for upper cuticle, except on veins which are marked by bands of rectangular cells in more or less longitudinal files. Trichome bases present on veins and rachises, sometimes between veins. Unicellular hairs have been observed.

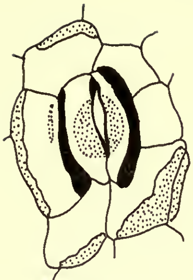
Stomata haplocheilic, densely disposed between veins on lower cuticle, typically monocyclic, sometimes imperfectly dicyclic, round or oval, having no definite orientation ; subsidiary cells often shared by two stomata. Guard cells little or not at all sunken. Subsidiary cells not much specialized, 6–7, not differentiated into polar and lateral, with cuticle considerably thickened on distal side (both periclinal and anticlinal walls). Guard cells cutinized, typically 40–50 μ long with dorsal and ventral walls sometimes thickened. A marked ring-shaped thickening surrounding aperture.

HOLOTYPE. LP 6233.

MATERIAL. In addition to the holotype, LP 6234–6249, BMNH, V.52266–75, LIL 2746–2752. Slides LP 167–173 ; BMNH, V.52276–78.

HORIZON AND LOCALITY. Lower Cretaceous, Baqueró Formation, lower member, *Araucarites* bed ; Estancia Bajo Grande, Santa Cruz Province, Argentina.

DESCRIPTION. *Pachypteris elegans* is a common element in the *Araucarites* bed of Bajo Grande. Its cuticle when macerated is yellow to pale brown in colour. The lower epidermis is readily distinguished by the presence of stomata which are completely absent on the upper cuticle. The guard cells are feebly cutinized and they present three pairs of rim-like thickened zones which surround the aperture. The inner, near the aperture (ventral) is the less marked. The outer thickening (dorsal), near the contact with subsidiary cell is well marked. Finally a median thickening between the inner and outer is sometimes developed and may be fused with the inner one. When present, it may be finely granular.



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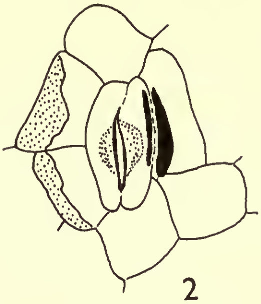

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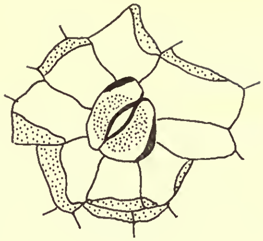

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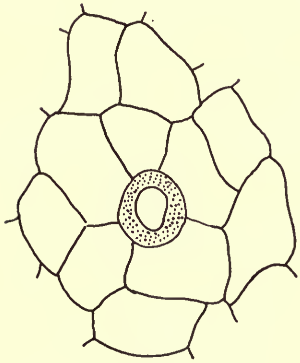

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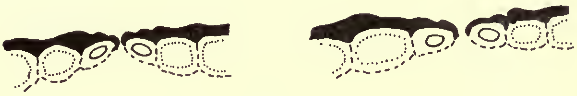

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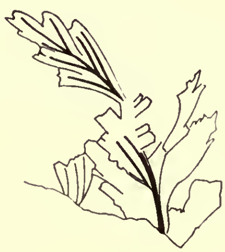

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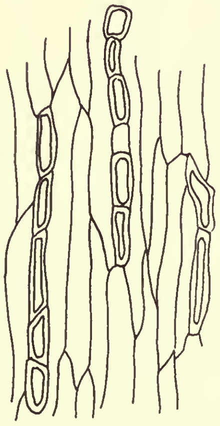

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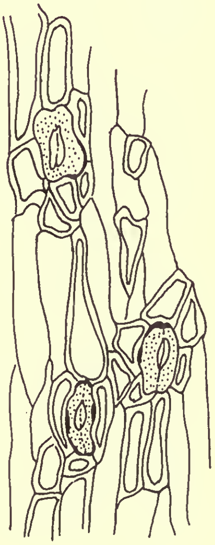

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FIGS. 1–5. *Pachypteris elegans* sp. n. Figs. 1–3, Stomata showing strong cutin thickenings (black) and less marked ridges (dotted) on guard cells and on subsidiary cells. Slide LP 169, ×370. Fig. 4, Hair base. Slide LP 169, ×370. Fig. 5, Section of stomata, ×370.

FIGS. 6–8. *Almargemia incrassata* sp. n. Fig. 6. Outline of holotype. LP 6255, ×1. Fig. 7. Portion of upper epidermis showing two types of cells. Slide LP 184, ×180. Fig. 8. Portion of lower epidermis showing stomata and two types of epidermal cells. Slide LP 184, ×180.

The stomatal aperture is slightly sunken, the poles of the guard cells being somewhat raised.

Stomata with only two large subsidiary cells have been seen.

Discussion. Harris (1964) emended the original diagnosis of *Pachypteris* (and included the genus *Pachydermophyllum* Thomas & Bose in it). This new diagnosis is based on general morphology of the frond as well as on its cuticular structure. The present species is included in *Pachypteris* because there is agreement in the shape of the fronds and their pinnules as well as in venation. There are, however, some differences in the cuticle: (a) the stomata are restricted to the lower epidermis in *P. elegans*, while those of the European species are amphistomatic (although very few stomata occur on the upper epidermis); (b) the guard cells of stomata are not much sunken in *P. elegans* and have thickened dorsal and ventral walls, plus the ring-shaped structure round the aperture. These differences characterize the new species, the third one with cuticle preserved (the other two being *P. lanceolata* and *P. papillosa*).

Among similar fern-like fronds from the Ticó flora, *Mesosingeria* although having comparable pinnules, differs in the lack of a definite mid-vein and in its cuticular structure, especially the stomata which are deeply sunken with a protective tube of cutine projecting outwards. *Ticoa* differs mainly in its stomatal apparatus (usually with a large epistomatal chamber) and in the shape of its epidermal cells which are normally elongated and not isodiametric. Moreover, the basal catadromic pinnules are never decurrent on the pinna rachis. The stomatal apparatus of *Mesodescolea* has in common the thickening of the guard cells on the dorsal walls as well as the median ring-like thickening, which is more pronounced. Ventral walls of subsidiary cells of this genus may also be thickened. In its gross morphology, the leaf of *P. elegans* is three times pinnate and has a fern-like appearance, while *Mesodescolea* is twice pinnate and has a wide pinnular lamina. There are some differences in cuticular structure. *Ruflorinia* also has guard cells with a median thickening round the aperture, but the shape of the guard cells is oval, corresponding to the shape of the stomatal apparatus. The lips of the guard cells are also different (strongly thickened) while no dorsal thickenings occur on these cells. The distribution of stomata and the number of subsidiary cells is markedly different.

Some species of the form genus *Scleropteris* (e.g. *S. pomelii* Sap.) may be compared with *P. elegans*, but as there is no information about the cuticle further comparisons are not possible. *Scleropteris* is a highly unnatural assemblage of species, probably uniting taxa of different natural orders (Archangelsky 1963*a*).

The peculiar thickenings on the guard cells of *P. elegans* are comparable with those found in the living Cycadales *Stangeria paradoxa* and *Bowenia spectabilis*. The stomata of both living genera have, like *P. elegans*, little or not at all sunken guard cells. The ventral walls of the guard cells are cutinized in all three taxa. *Stangeria* and *P. elegans* have dorsal walls of subsidiary cells with cutinized ridges (sometimes in the fossil species there are two parallel ridges of cuticle, one on the guard cell and the other on the limit of guard and subsidiary cell). The median ring-like thickenings on the guard cells are absent in *Stangeria* but may be seen in *Bowenia*. In all three taxa the stomata are monocyclic to imperfectly dicyclic. The external morphology of the leaves in *Stangeria* and *Bowenia* differs considerably from the fronds of *Pachypteris elegans*.

This Patagonian fossil may well be one of the latest representatives in Southern floras of that imperfectly known group of " Mesozoic Pteridosperms ", which on the one hand has some similarities with the true Cycadales while on the other has characters of its own. The fructification *Pteroma* (Harris 1964) which is supposed to be the microsporophyll of *Pachypteris papillosa*, may throw some light on the true relationships of this group.

Genus ***ALMARGEMIA*** Florin 1933

Almargemia incrassata sp. n.

(Pl. 1, figs. 3, 4 ; Pl. 3, figs. 13, 14 ; Text-figs. 6–10, 13)

DIAGNOSIS. Leaf (fragmentary) simply pinnate. Rachis delicate, 1·5 mm. wide. Pinnae subopposite, inserted at angle of about 45° (more acute towards apex), with decurrent catadromic side and constricted anadromic side, oblong, with broadly dentate apex, up to 1 cm. long × 0·4 cm. wide at the middle ; lateral margins dentate towards apical sector. Uniform veins, 3–4 per pinna, parallel to margins, converging at base. Fine lines between veins clearly differentiated.

Both cuticles 2 μ thick, with markedly elongated and similar epidermal cells, about 20 μ wide. They are of two kinds : (1) numerous, with thin anticlinal walls (1 μ) and (2) less numerous, with thick anticlinal walls (7 μ), and less elongated. The thick-walled cells form longitudinal rows one, or occasionally more than one, cell broad. Cells on rachises markedly elongated with the same two types of thin and thick-walled cells and occasional papillae on the thick-walled cells.

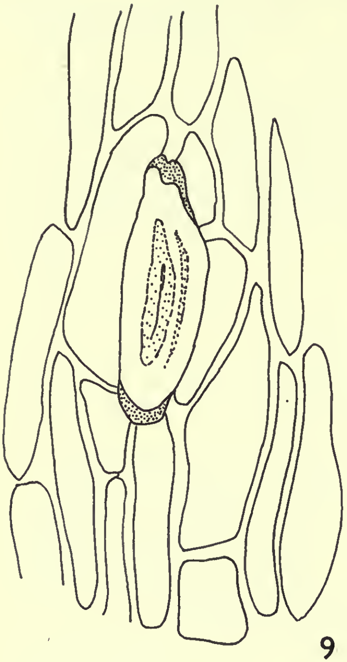
Stomata present on lower cuticle only, longitudinally orientated, sometimes obliquely, placed in rows of thick-walled cells, typically monocyclic to imperfectly dicyclic. Subsidiary cells typically 4–6 in number. Polar subsidiary cells occasionally differentiated ; longer than lateral subsidiary cells which sometimes slightly overhang guard cells. All subsidiary cells usually thick-walled (there are a few exceptions). Stomata sometimes with subsidiary cells in contact. Guard cells with poles on epidermal surface and aperture slightly sunken, 50–55 μ long. Poles, ventral and dorsal walls strongly cutinized. Longitudinal ridge of cutin occasionally present near dorsal wall of guard cells.

HOLOTYPE. LP 6255.

MATERIAL. In addition to the holotype, LP 6254 ; BMNH, V.52264. Slides. LP 184 ; BMNH, V.52265.

HORIZON AND LOCALITY. Lower Cretaceous, Baqueró Formation, lower member, *Araucarites* bed ; Estancia Bajo Tigre, Santa Cruz Province, Argentina.

DESCRIPTION. *Almargemia incrassata* sp. n. is represented by only two fragmentary specimens. LP 6254 is a leaf fragment about 3 cm. long. It shows a few pinnae on both sides of a slender rachis. The pinnae are poorly preserved but show the



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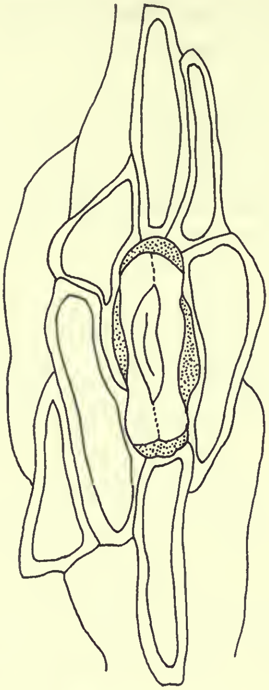

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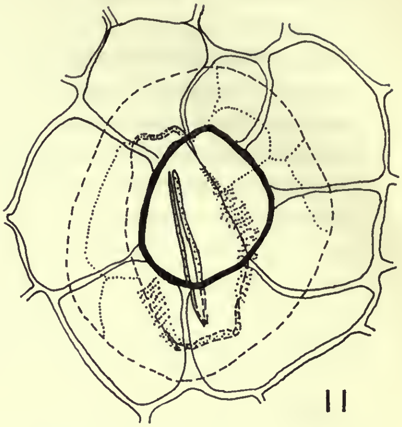

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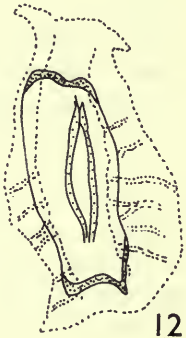

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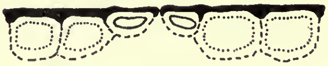

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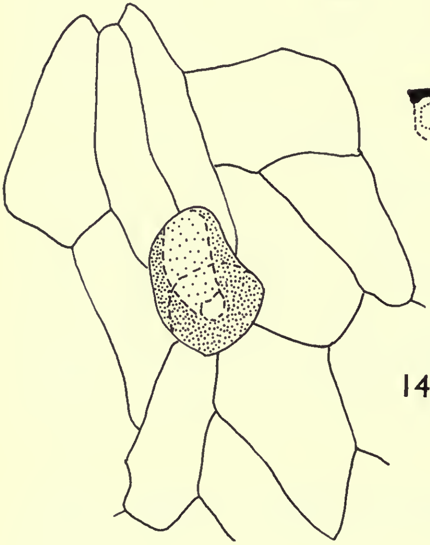

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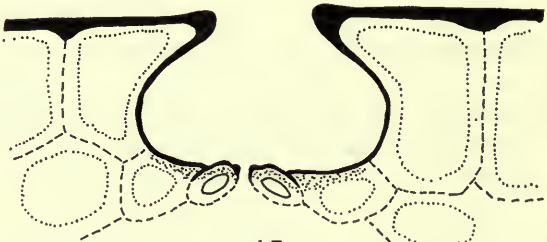

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FIGS. 9, 10, 13. *Almargemia incrassata* sp. n. Figs. 9, 10. Stomata. Slide LP 184, ×500. Fig. 13. Section of stoma, ×500.

FIGS. 11, 12, 14, 15. *Ticoa lamellata* sp. n. Fig. 11. Stoma showing sunken guard cells, large pit and remnants of lamellae. Slide BMNH. no. V.52263, ×500. Fig. 12. Guard cells of a stoma showing remnants of lamellae. Slide LP 174, ×500. Fig. 14. A trichome. Slide BMNH. no. V.52263, ×500. Fig. 15. Section of stoma, ×500.

main morphological characters. The cuticle is well preserved and is resistant to maceration, after which it remains as an almost colourless film. The other leaf fragment (LP 6255) bears three complete pinnae, clearly showing the shape with its characteristic dentate margins. The fine lines between veins mentioned in the diagnosis clearly correspond to rows of thick-walled epidermal cells. This character of thick and thin walled cells on the same epidermis is known to occur among Recent Cycadales and has been fully discussed by Pant & Nautiyal (1963). The stomata are typically exposed with their poles of guard cells curved towards the surface, while the aperture is slightly sunken. This character, which is also common to both living and fossil Cycadales, is also found in the genus *Ticoa* although not so sharply marked as in *Almargemia.* The ventral and dorsal thickenings of the guard cells are conspicuous ; the contact area between guard and subsidiary cells (dorsal wall of guard cells) is also thickened, usually a little less than the other thickenings mentioned. In a few cases, guard cells with strong dorsal ridges parallel to the dorsal walls of the guard cells were observed. Also the subsidiary cells may slightly overhang the guard cells. All these characters related to the thickenings of the guard cells are found in most of the living Cycadales. Thus *Almargemia incrassata* is another element of the Ticó flora which may be placed in or near the Cycadales, in its strict sense, and agrees with Florin's (1933) observations on the type species of the genus, *A. dentata* (Heer) Florin.

Discussion. Among fossil leaves with a similar pinnate plan, *A. incrassata* is most similar to the type species of the genus, *A. dentata* (Florin 1933 : 100). Leaves of the European species are pinnate with dentate margins, and are borne on slender rachises with a similar plan of venation. Differences in morphology are of specific significance : the size of the pinnules and the number of veins is greater in *A. dentata,* while in *A. incrassata* the margins of pinnae are more dentate. The cuticles agree in having epidermal cells of two sorts, but in *A. incrassata* thick walled cells form definite longitudinal rows while in *A. dentata* they are usually isolated or occur in small groups. Stomata of both species are typically surrounded by thick-walled cells with 4–6 subsidiary cells. The guard cells are alike in both species.

Teixeira (1948) figures *A. dentata* from Almargem (pl. 18, figs. 9–11) and from Belas (pl. 21, figs. 4–7), but adds no diagnostic characters to the original description. In these specimens, the shape of the pinnules is clearly different from *A. incrassata. A. dentata* is recorded from the Lower Cretaceous (Aptian) of Portugal. Thus the geographic distribution of the genus and probably its geological range are extended.

Genus ***TICOA*** Archangelsky 1963

Ticoa lamellata sp. n.

(Pl. 1, figs. 2, 8, 9 ; Pl. 3, figs. 15, 16 ; Text-figs. 11, 12, 14, 15)

Diagnosis. Leaf at least bipinnate. Segments incomplete, at least 3 cm. wide with rachis 2 mm. wide. Pinnae lanceolate up to 1·4 cm. long × 0·5 cm. wide, ending with acute pinnule, inserted at an angle of about 75°, alternate, slightly overlapping adjacent pinnae. Pinnules alternate, inserted at an angle of about 70°, up to 4 mm. long × 1·5 mm. wide, slightly decurrent, lanceolate, constricted at base. Those towards proximal part of pinnae (near rachis) more oblong, with rounded apex and margins entire (not lobed). Veins not seen.

Both cuticles of similar thickness, 3 μ. Upper cuticle having no stomata but numerous trichomes. Cells markedly elongated, parallel to margins, with straight walls. Cells of lower cuticle elongated near margins and on veins, somewhat isodiametric or wedge-shaped near stomata and trichomes, slightly elongated on rest of lamina. Cell surface flat; anticlinal walls straight, sometimes pitted. Cells on rachises markedly elongated; trichomes and elongated stomata present. Anticlinal walls thicker than those of lamina.

Stomata usually dicyclic, avoiding veins and margins, longitudinally orientated, parallel to veins and margins, 25–40 per sq. mm. Guard cells strongly sunken in round or oval pit, formed by subsidiary and encircling cells. Encircling cells typically 6–8, forming sides of pit, about 40–50 μ wide. Mouth of pit typically 40–50 μ wide, situated at the same level as epidermis or slightly raised. Subsidiary cells small, at bottom of pit; guard cells 50–60 μ long, well cutinized, with cutin thickenings on dorsal and ventral walls. Poles of guard cells raised and strongly cutinized. Transverse striations occur on dorsal walls of guard cells, extending on both sides. They may belong to the remnants of lamellae.

Trichomes single, sometimes in pairs, composed of an isodiametric cell, 25–35 μ in diameter, with thick anticlinal walls, about 7–9 μ. Free part composed of single cutinized hair with thick lateral walls.

Holotype. LP 6250.

Material. In addition to the holotype, LP 6245*b*; BMNH, V.52262. Slides LP 174; BMNH, V.52263.

Horizon and locality. Lower Cretaceous, Baqueró Formation, lower member, *Araucarites* bed; Estancia Bajo Grande, Santa Cruz Province, Argentina.

Description. The material consists of fragmentary specimens preserved as black compressions on a pale grey matrix. When macerated the cuticle appears as a pale yellow film and is quite resistant to chemical treatment. The impressions of the pinnules show no traces of veins. However, on the lower cuticle a median longitudinal strip devoid of stomata may well represent the mid-vein. Lateral veinlets were not observed.

Discussion. This species is closely comparable with *Ticoa harrisii* in the size of pinnules. However *T. lamellata* has pinnae and pinnules inserted at a wider angle (70–75° against 45° in *T. harrisii*). Pinnules of the new species are usually constricted at the base; no lobation of basal pinnules was seen. The cuticle is of the same thickness on lower and upper epidermis while in *T. harrisii* the upper cuticle is thicker than the lower. The stomatal number is slightly higher in *T. lamellata* while the number of encircling cells is lower (6–8 against 8–10 in *T. harrisii*). Hair bases in *T. lamellata* do not show inwardly cutinized extensions as seen in *T. harrisii* and *T. magnipinnulata*. Finally, the guard cells in *T. lamellata* have their poles more strongly cutinized; also, the probable remnants of lamellae while constant in the new species, were not observed in the others. *T. magnipinnulata* on the other hand, differs in the size and shape of pinnules as well as in stomatal structure (it has 3 cycles of cells forming the stomatal pit).

Ticoa is another leaf genus whose leaves may be compared with those of other genera so far as their shape is concerned. All three species are alike in cuticular and especially in stomatal structure. The shape and size of leaves, however, are more varied, *T. harrisii* and *T. lamellata* being closer to each other than to *T. magnipinnulata*. The two former species may be compared with *Pachypteris* only in the shape of pinnules, although the lamina of basal pinnules does not extend to the segment rachis. The cuticles of the two genera differ in the shape of their epidermal cells and in stomatal structure. Trichome bases with cutinized anticlinal walls are constantly present in *Ticoa* but absent in other similar leaf genera.

Coniferales

The six species of conifers so far known in the Ticó flora have been referred to the genera *Brachyphyllum*, *Athrotaxis* and *Tomaxellia*. Most of them are numerically important in the different beds of the Ticó Amphitheatre. Other conifers were subsequently found in Bajo Tigre and Bajo Grande, and some of them will be described here. Isolated ovuliferous scales are referred to the Araucariaceae, confirming the presence of this family in the Ticó flora. The Podocarpaceae are represented by several species, some with male and female structures. The suspected presence of this family (Archangelsky 1963) is therefore also confirmed. A new species of *Tomaxellia* is also described.

The Podocarpaceae and the Araucariaceae appear to be the best represented families of conifers in the Lower Cretaceous of Patagonia. They are represented by numerous species each with a large number of individuals. Many other conifers have been collected from different localities of the Ticó flora (some of them probably belonging to these families). The pollen content of some beds shows a high number of bisaccate pollen grains (as well as trisaccate) which may well have been derived from species of the Podocarpaceae.

Family **ARAUCARIACEAE**

Genus ***ARAUCARITES*** Presl 1838

The generic name *Araucarites* is used for cones, isolated ovuliferous scales and sterile twigs having " araucarian affinity " (Seward 1919 : 256). While it is possible to relate female structures with some security to the living Araucariaceae, the assignation of sterile twigs is less secure even when the cuticular structure is preserved.

The two species described here are isolated ovuliferous scales showing a single median embedded ovule and a ligule supported by wide lignified bracts.

Araucarites baqueroensis sp. n.

(Pl. 1, fig. 5 ; Text-fig. 17)

1951 *Araucaria* (section *Colymbea*), Feruglio : 65.

Diagnosis. Cuneiform ovuliferous scale with lateral wings and acuminate apex about 3 mm. long. Width of scale 2 cm., length 2–3 cm. A single oval seed immersed in the scale is typically 1–1·5 cm. long × 4–5 mm. wide, broadest near distal end. Delicate wings expanded laterally up to 0·8 cm. from edge of seed. Ligule short, not exceeding external margin of bract, maximum width about 1 cm.

Holotype. LP 5766*b*. (Cerro Testigo bed.)

Material. In addition to the holotype, LP 5767*b*, 5768*b*, 5770 (Cerro Testigo bed) ; LP 6345–46 ; BMNH, V.52254 (*Araucarites* bed) ; LP 5277*b* (*Cladophlebis tripinnata* bed) ; LP 5369*c* (*Ticoa harrisii* bed).

Horizon and locality. Lower Cretaceous, Baqueró Formation, lower member. Estancia Bajo Tigre (Cerro Testigo bed) ; Estancia Bajo Grande (*Araucarites* bed) and Ticó Amphitheatre (*Cladophlebis tripinnata* and *Ticoa harrisii* beds), Santa Cruz Province, Argentine.

Description. *Araucarites baqueroensis* is based on numerous ovuliferous scales from different localities, those from the Cerro Testigo bed in Bajo Tigre yielding the most abundant and best preserved. They are usually fragmentary and are associated with abundant broad twigs referred to *Brachyphyllum*. Only impressions were found in this bed which consists of a fine-grained, pale brown sediment, similar to the Ticó or other Bajo Tigre horizons bearing mummified plant fragments. However, in this bed oxidation has destroyed all cuticles.

The scales are large, much larger than those of the other species, *A. minimus* from Bajo Grande. In *A. baqueroensis* the ligule is well defined, being separated laterally from the wing of the bract by a visible ridge (which is a mould of the cavity left in the original compression, between the tissue of the bract and the ligule). Near the apex, the ligule is broader but does not exceed the length of the bract. The field between the external distal margin of the bract and the seed is large, more than 5 mm. long. Most specimens are broken ; seeds or seed ligules are commonly found isolated from the bract, but a few specimens show clearly the seed ligule and their bracts which have wing-like lateral expansions. The acuminate apex is usually broken but can be seen in some specimens projecting for a short distance. Two fragmentary remains of what I believe to be the same species were found in Bajo Grande. One of them (LP 6346) shows a distinct acuminate apex of the bract projecting for 3 mm., distally broken. The specimen from the *Cladophlebis tripinnata* bed in Ticó is also fragmentary but agrees with the typical material. The one from the *Ticoa harrisii* bed is slightly larger (about 3 cm. long, incomplete), and shows the characters of the species.

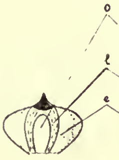
Discussion. *Araucarites baqueroensis* differs in size and shape from the other species (*A. minimus*) described in the present paper.

Araucaria sp. as described by Berry (1924) from the Jurassic of Santa Cruz

Province (Argentina) is similar in size and general shape, but the ligule appears much narrower than in the present species, especially in its distal sector.

Feruglio's *Araucaria* sp. from Cerro Cuadrado and Punta del Barco may well belong to *Araucarites baqueroensis*, but only a brief description and no figures are available. It was found in the same formation but in the upper member where the plant association is somewhat different.

Some specimens from Graham Land described as *Araucarites cutchensis* Feistm. by Halle (1913*a*, pl. 8, figs. 5, 7, 8) are similar in size and shape but they have a pointed acuminate apex and a narrower ligule. The type specimens described by Feistmantel (1876) are also similar to *A. baqueroensis* but they show a long acuminate apex (Feistmantel 1876, pl. 9, fig. 1), although this is lacking in some of the specimens. In subsequent publications, the same author included markedly different forms in this species (cf. Feistmantel 1877, pl. 14, figs. 6, 8).



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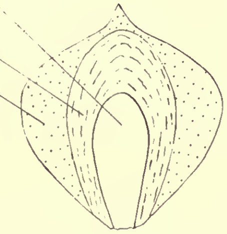

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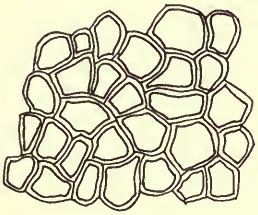

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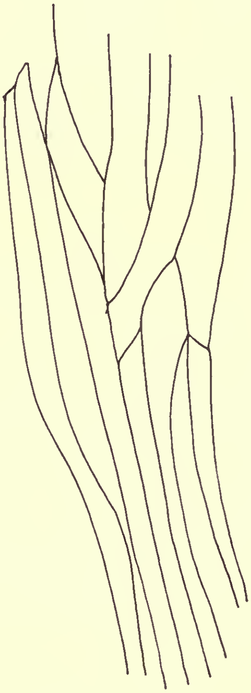

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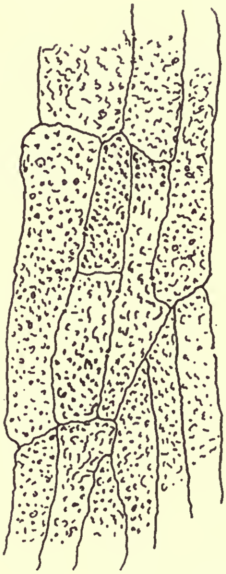

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FIGS. 16, 18–20. *Araucarites minimus* sp. n. Fig. 16. Ovuliferous scale (reconstructed), ×1. *o*, ovule ; *l*, ligule ; *e*, bract. Fig. 18. Cells of outer membrane. Slide LP 233, ×370. Fig. 19. Cells with straight and unpitted walls of membrane (3) of diagnosis. Slide LP 235, ×370. Fig. 20. Cells of granulose membrane (2) of diagnosis. Slide LP 234, ×370.

FIG. 17. *Araucarites baqueroensis* sp. n. Ovuliferous scale (reconstructed), ×1. Lettering as for Fig. 16.

Araucarites minimus sp. n.

(Pl. 1, figs. 6, 7; Text-figs. 16, 18–20)

DIAGNOSIS. Broadly cuneiform ovuliferous scales with well developed lateral wings and acuminate apex up to 3 mm. long. Width of scale typically 8 mm. length at least 7 mm. broken at base of attachment. Single oval seed immersed in scale, typically 3·5–5 mm. long × 2–2·5 mm. wide, broadest near distal end. Delicate wings expanded laterally up to 3·5 mm. from edge of seed, with irregularly lobed margins, showing sinuous bands of probably fibrous cells. Short ligule, not exceeding external margin of bract, about 3–4 mm. wide, sometimes seen.

Four cutinized membranes present: (1) Outside of scale, including outside of integument of seed, rather strong, finely granular with more or less isodiametric cells, about 20–30 μ in diameter, usually with rounded contours and thick anticlinal walls (up to 4 μ). Membrane on wings becoming very delicate and losing all traces of cell contours. Dark contents usually adhering to this membrane, forming definite bands disposed in close files. (2) Thin granular membrane showing markedly elongated cells, 15–20 μ wide, with anticlinal pitted and minutely crenulate walls. (3) Thin membrane with markedly elongated cells, 5–15 μ wide, but showing no granules on surface, with straight, unpitted walls. (4) Structureless strong membrane, probably corresponding to megaspore wall.

HOLOTYPE. LP 6329.

MATERIAL. In addition to the holotype, LP 6328, 6330–44; LIL 2739–2745; BMNH, V.52255–60. Slides LP 231–235; BMNH, V.52261.

HORIZON AND LOCALITY. Lower Cretaceous, Baqueró Formation, lower member, *Araucarites* bed; Estancia Bajo Grande, Santa Cruz Province, Argentina.

DESCRIPTION. *Araucarites minimus* is abundant in Bajo Grande. The delicate wings may be lacking, but this is probably an accident of preservation. The size of the seed is fairly uniform. The seed is embedded in the scale and covered by its surface. It occupies a hollow cavity which may be filled with mineral substances (powdery calcite or limonite) or preserved as a carbonized body. These coal fragments when treated with dilute alkali show three types of membranes (membranes 2–4 of the diagnosis). The two membranes with narrow and elongated cells might both belong to the nucellus cuticle but I prefer merely to designate them as membranes 2 and 3 until more material shows their true nature. The rest of the scale is also covered by a carbonaceous film which is broken into small fragments. These fragments after treatment with dilute alkali, show the same type of membrane, assumed to be the outside of the scale. It is similar on the acuminate apical sector, on the base and top of the seed. The ligule is usually broken, but in a few specimens it is seen to be similar to that of *Araucarites phillipsii* described by Kendall (1949: 155, text-fig. 1B).

DISCUSSION. I have referred these scales to the Araucariaceae because they have one seed and the remnants of a ligule embedded in the bract. The size of the scales makes it possible to estimate the approximate size of the female cone, which might have been about 2 cm. in diameter (relatively small for the Araucariaceae). Most of the living species have large cones and so has the fossil *Araucaria mirabilis* (Spegazzini) described and figured by Calder (1953) from the Jurassic of Santa Cruz Province. Furthermore, it is possible to include *A. minimus* in the *Eutacta* section of the genus *Araucaria*, because the scales of the other two sections, viz. *Bunya* and *Colymbea* are of a different type. As already pointed out by Berry (1924) and others, it is curious that the two living representatives of the family in South America, *Araucaria araucana* (Mol.) K. Koch and *A. angustifolia* (Bertolini) O. Kuntze, belong to the *Colymbea* section, while all fossil representatives so far found in the same area may be classed in the *Eutacta* section, including the two species from Ticó.

Fossil material referred to *Araucarites* (cone scales) has been described from Jurassic and Lower Cretaceous strata in South America. Halle (1913*a*) describes several female cone scales from the Middle Jurassic of Graham Land. All this material is included in Feistmantel's *Araucarites cutchensis* described from the Jurassic of India which represents a rather unnatural assemblage. All the figured specimens (Halle 1913*a*, pl. 8, figs. 3–8) are much larger than ours and have a longer acuminate apex. The original description of *A. cutchensis* is poor, but judging from Feistmantel's (1876) figures *A. minimus* differs in shape and is much smaller. The specimens of *A. cutchensis* figured by Feistmantel (1877) are also different in size and shape. There are also differences in the shape of the scales figured by Feistmantel (1879), although they are closer in size to *A. minimus*. *Araucarites macropterus* Feistmantel is much larger than *A. minimus*.

Berry (1924) described cone scales of *Araucaria* sp. from the Laguna del Carbón, in the Gran Bajo de San Julián, Santa Cruz Province.[1] These scales differ in shape and size from *A. minimus* by having a less developed wing and a shortly acuminate apex. Feruglio (1951) described scales of *Araucaria* from the Laguna del Molino of the Gran Bajo de San Julián, Santa Cruz, which he considered as Upper Jurassic or Lower Cretaceous. No figures were given, but the description suggests that they are larger. In the same paper, Feruglio briefly described other scales from the Punta del Barco and Cerro Cuadrado localities, comparing his material with that described by Berry (1924), and therefore different from ours.

Araucarites nipaniensis Singh (1957) from the Jurassic of India, although only slightly larger than *A. minimus* differs in the shape of the seed and in having a large distal field between seed and margin of bract. No acuminate apex has been reported in this species.

Araucarites phillipsi Carruthers from the Jurassic of Yorkshire, as described by Kendall (1949) is larger (up to 1·7 cm. long). It agrees in having a short ligule but the acuminate apex of the bract is not as prominent as in our species. The wings in *A. minimus* are also more developed. The epidermis of the cone scale differs in its more elongated cells but the cells of the nucellus cuticle are similar and so is the megaspore membrane.

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[1] I have doubts as to the age of these sediments which Berry described as Rhaetic. Feruglio (1951) considers that the Gran Bajo de San Julián strata which contain these plants are either Jurassic or Lower Cretaceous. Stipanicic (1957) in a complete geological survey of this area, concludes that the Laguna del Carbón section (as well as all other similar exposures in the Gran Bajo de San Julián) belong to his Matilde Formation, Middle to Upper Jurassic in age. The facts given to ascertain this age are not conclusive ; there are few plants, most of them useless for precise age determination, such as *Cladophlebis*, *Sphenopteris*, *Ptilophyllum* and *Podocarpus*. The mention of *Athrotaxis* cf. *ungeri* points to a relation with the Baqueró Formation or similar strata from the Lago San Martin area, also in Santa Cruz Province.

Family **PODOCARPACEAE**

Genus ***TRISACOCLADUS*** nov.

Derivation of name. *Trisaco*, three air bladders of the pollen grains, *cladus*, leaf.

Diagnosis. As for the only species, *Trisacocladus tigrensis* sp. n.

Trisacocladus tigrensis sp. n.

(Pl. 4, fig. 21 ; Pl. 5, figs. 22–39 ; Pl. 8, figs. 56–67 ; Text-figs. 21–25)

Diagnosis. Twigs branched, widest seen 0·6 cm. and longest 5 cm. (base and apex broken). Leaves disposed in a close spiral, when detached from branch leaving a marked rhomboidal cushion with a slight depression, probably representing the vascular supply. Leaves radially disposed or spreading in one plane, with rounded apex, decurrent, with margins entire, typically 5–6 mm. long × 0·8 mm. wide. A median longitudinal depression suggesting the mid-vein sometimes seen. Substance of lamina thick.

Male cones axillary, attached and shortly pedunculate, oval, gradually tapering towards apex, smallest seen 9 mm. × 3 mm., largest 15 mm. × 4·5 mm. Central axis straight, up to 2 mm. wide. Microsporophylls spirally arranged, inserted at right angles to axis (sometimes more than 90°) composed of a main branch expanding at distal end into a head also placed at right angles (parallel to cone axis). Head extending upwards as short laminar projection, up to 3 mm. long, covering base of next sporophyll. Head also extending downwards as short keel. Two (or more?) oval pollen sacs present, up to 1 mm. long. Cuticle of sporophyll delicate, showing more or less elongated cells, 10–15 μ wide, with straight walls. Membrane of pollen sac appearing structureless and irregularly granulose. Pollen usually of *Trisaccites* type, varying in shape and size from 12–32 μ in equatorial diameter. Equatorial outline somewhat triangular, sometimes round or oval. Three (sometimes two) small air bladders usually present on distal half of body. Exine of body appearing psilate or faintly foveolate, while on wings it may be reticulate. Margins of air bladders finely crenulate.

Female cone-like structures probably laterally inserted on branches, subtended by a few sterile leaves. Longest cone seen 2 cm. × 7 mm. wide. Central fleshy axis, 2–6 mm. wide, bearing irregularly (or bilaterally?) erect ovules (and small linear bracts up to 5 mm. long?). Ovules orthotropous, close together, typically oval, 2–3 mm. long × 1·5–2 mm. wide composed of three cutinized layers : (1) innermost delicate membrane, finely granular, showing no structure, assumed to be the megaspore wall ; (2) thin membrane showing elongated narrow cells, 5–15 μ wide, projecting into short acuminate apex ; cells becoming much shortened towards base and apex, assumed to be the nucellus ; (3) outer membrane showing no structure but many circular granules irregularly disposed or tending to form ill-defined files assumed to be the integument. Impressions of ovules show longitudinally elongated bulging meshes crowded with small circular granules, tending to be disposed in files.

Seeds developing a stone, showing a marked micropilar projection and meshes on outer surface, crowded with small granules.

HOLOTYPE. LP 5826 (*Trisacocladus* bed).

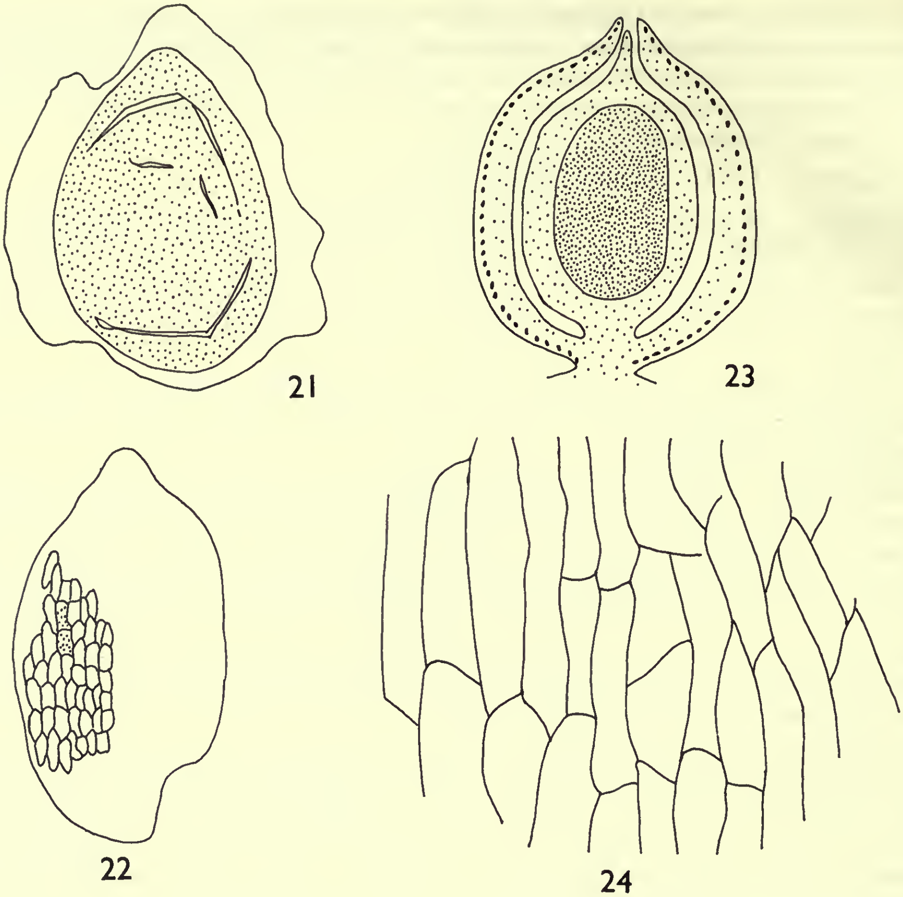
MATERIAL. In addition to the holotype LP 5827–42, 5844–50, 6157–69, 6175–81, 6211–32; BMNH, V.52235–38, V.52240–50, V.52252–53 (*Trisacocladus* bed); LP 6182–91 (*Ginkgoites tigrensis* bed); LP 5818*b*, 6170–74, 6430–39; BMNH, V.52239, V.52251 (Upper bed). Slides LP 54–65, 155–166, 244, 300–302; BMNH, V.52234.

HORIZON AND LOCALITY. Lower Cretaceous, Baqueró Formation, lower member, *Trisacocladus*, *Ginkgoites tigrensis* and Upper beds. Estancia Bajo Tigre, Santa Cruz Province, Argentina.

DESCRIPTION. This plant occurs in a newly discovered bed of the Bajo Tigre here referred to as the *Trisacocladus* bed. Deep horizontal tunnels made by coal miners enabled me to collect abundant material. The bed extends horizontally and is located on the roof of these tunnels. It yielded abundant *Trisacocladus tigrensis* branches and cones and also freshwater phyllopods but no other fossils. The rock is pale brown in colour and the fossils are dark brown. The matrix is fine grained, but a few centimetres below this layer the grain becomes coarser and the rock includes many coal fragments, some of considerable size.

Numerous branches have radially disposed leaves but one specimen shows leaves spreading in one plane. Both types are here considered as belonging to the same plant. No trace of cuticle was found. All attempts, including transfers, failed. The leaves are usually covered by a very fragile film which may be the mineralized remnant of the cuticle, but it shows no structure. The phyllotaxis of the leaves is probably 3/8. Fragments of this conifer were also found in other beds of Bajo Tigre (*Ginkgoites tigrensis* and Upper beds, about 5 metres above).

The holotype shows clearly the attachment of a male cone to a short fragmentary branch. On the axis of this attachment a few linear leaves up to 6 mm. long are present, and they are comparable to those found on the sterile branches. All the other male cones were found isolated. As their shape, size and pollen content are very similar to the holotype, they are all placed in *Trisacocladus tigrensis*. It is not clear whether the pollen sacs are placed on the adaxial or abaxial surface of the sporophyll, but as they are believed to be of podocarpaceous affinity, I presume their position is abaxial. Many cones have their pollen sacs still preserved as coaly oval bodies which may be easily separated and treated with very dilute alkali. In such sacs the pollen is also well preserved. Similar cones yielding pollen grains of the same type are also found in the *Ginkgoites tigrensis* bed associated with comparable sterile twigs. One of these cones (LP 6184) has at its base a few leaves similar to those described for the holotype. In the Upper bed, *Ginkgoites* is missing while *Trisacocladus* becomes abundant. Many twigs and male cones are found in associa-



FIGS. 21–24. *Trisacocladus tigrensis* gen. et sp. n. Fig. 21. Two membranes seen on a translucent specimen. Inner (dotted) belongs to the megaspore membrane; the outer is the nucellus membrane. Slide LP 159, ×25. Fig. 22. Outlines of the elongated bulging meshes (two with crowded small granules) seen in impressions of seeds. LP 5849, ×25. Fig. 23. Ideal section of the ovule showing megaspore membrane, nucellus and integument (with inner content). ×25. Fig 24. Cells of cuticle of the microsporophyll. Slide LP 50, ×370.

tion. The pollen grains and the gross morphology of twigs and leaves are in all respects similar.

When preparing the pollen sacs, many grains were found still attached to the irregularly granulose membrane, although most of them spread free when the sac burst. The three small air bladders give the grains a typical appearance, similar to the sporomorphs described as *Trisaccites* from Australia, Tasmania and New Zealand (Cookson & Pike 1954, Couper 1960). In the present material the bladders are flattened in the distal half of the body (unexpanded). However, in the same pollen sacs a few grains with turgid bladders have been found. Such grains closely resemble the sporomorph *Microcachrydites*, found also in Australia, New Zealand, Tasmania and Antarctica. A detailed study of the pollen grains from Bajo Tigre has been published by Gamerro (1965).

Only one specimen (LP 5846) shows what may be an organic attachment of a female cone to a shoot bearing *Trisacocladus tigrensis* leaves. A few leaves are placed in the axil of the shoot and the presumed base of the cone.

The typical fleshy axis of the cone is conspicuous and shows many adhesions, mainly quartz grains and *Triletes* type megaspores ; it was probably sticky for irregularly placed leaf fragments are also found glued to the surface. There is little doubt that the axis was originally cylindrical. It usually bears ovules on two sides of the compression, but in some specimens they occur in other positions. Some axes show definite scars which may belong to the bases of fallen ovules. If this is true, then the cone axis was covered by radially disposed ovules. No bract or any sterile appendage was seen in relation to the ovules and the axis. Some sterile linear bracts (or leaves?) may be seen crossing the exposed surface of the cone axis, but only in a few specimens, and I am not sure that they bear any relation to the ovules (Pl. 5, fig. 39).

The ovules are erect and show no covers or outgrowths. The integument is thick and possibly had some cell contents which formed the granules mentioned in the diagnosis. The nucellus is strongly cutinized down to near the base (chalaza), its cells near the base and apex being much shorter than at the middle. The anticlinal walls are also more strongly cutinized towards the base and apex.

The ovules still attached to the cone axis have some of their membranes preserved, and they were treated in the usual way with dilute alkali. They show the three membranes of the diagnosis, the inner and structureless one being the megaspore wall. The chalaza is clearly seen in some specimens, being somewhat elliptical and transversely elongated (probably the ovules were somewhat flattened). The scars seen on the axis are similar in size and shape and may correspond to the chalaza.

Detached seeds referred to *T. tigrensis* are preserved in two ways :

1. The stone is well developed within a cavity and shows the characteristic meshes on its outer surface. Usually no inner cuticle is preserved.

2. The seed is flattened as a disc from which good cutinized membranes can be obtained. The meshes on the outside are usually seen clearly. The stone is not preserved as a separate recognizable layer. Seeds still attached to the cone axis are always preserved in this manner.

Similar venation in the preservation of conifer seeds has been noted occasionally in other floras. Where the external meshes are seen clearly they distinguish the seed of *T. tigrensis* from that of the associated *Karkenia incurva* Archangelsky (1965).

These cones are identified with the foliage already described as *Trisacocladus tigrensis* for the following reasons : (1) there is one specimen which shows what I believe is an organic connection ; (2) in the bed where these cones occur, only this type of foliage and male cones are known and no other plant remains have so far been found, among hundreds of vegetable fragments ; (3) in a lower bed, where *Ginkgoites* *tigrensis* is abundant, *Trisacocladus tigrensis* foliage and male and female cones also occur. (4) In another (Upper) bed which is probably a lateral equivalent to the *Trisacocladus* bed, distant about 700 metres from it, seeds of the cones and shoots plus male cones also occur together. Thus, these elements are associated in three different beds and there is one probable organic connection.

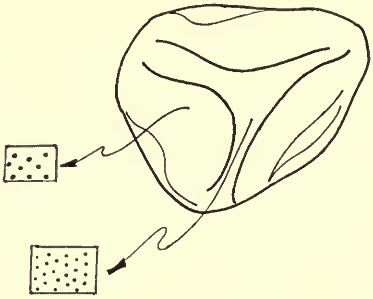
Discussion. In the absence of cuticle it is not possible to relate *Trisacocladus* with *Tomaxellia*, which occurs in the same formation but at different localities. There is agreement in the shape of leaves, although individual leaves of *Trisacocladus* are smaller. In *Tomaxellia* leaves spreading in one plane were not observed. All *Elatocladus* species described by Halle (1913*a*) from Hope Bay, Graham Land, are different. *E. heterophylla* is somewhat similar but differs in having leaves with an acute apex (on both short and long leaves) and in the variation of the size of the leaves found on different shoots (not so marked in *Trisacocladus tigrensis* as in *E. heterophylla*). There is also a difference in age, the Antarctic species being probably Middle Jurassic.

The male cones of *T. tigrensis* are of the type usually referred to the organ genus *Masculostrobus*. Several species of this genus are known from Jurassic and Cretaceous strata. Only one, *M. sahnii* Vishnu Mittre (1956) from the Jurassic of India, has pollen grains bearing three air bladders. The Indian cones are smaller (7 mm. × 3 mm.). Pollen grains usually bear 3 bladders, but 2 or 4 were also seen. The equatorial diameter of the grains is somewhat greater (32–39 μ against 12–32 μ in the present species). A few leaves on the basal portion of the cone of *M. sahnii* are known. They agree in shape with those of *Trisacocladus tigrensis*, but are smaller.

Vishnu Mittre (1957) considers that the female structures of *M. sahnii* probably belong to *Nipanioruha granthia* Rao discussed later. Pollen grains similar to those found in the cones, were observed in many preparations of dispersed pollen grains in sediments of other beds. They are commonly preserved with unexpanded air bladders and subtriangular equatorial outline. It is interesting to note that *Trisaccites* grains (like ours) are known from Upper Jurassic, Cretaceous and Early Tertiary sediments of Australia, New Zealand and Tasmania. The same geological range applies to *Microcachrydites*, another palynomorph, which has been found in the same localities and also in Antarctica (Cookson 1947).

Among Recent conifers *Trisacocladus* can be matched only within the Podocarpaceae. The leaves are similar to those found in *Podocarpus* and *Dacrydium*. Its male cones resemble in shape some cones of *Podocarpus*, but there is a clearly defined sporophyll axis in *Trisacocladus* instead of a more or less laminar microsporophyll found in Recent Podocarpaceae. On the other hand, pollen with three air bladders is found in some *Podocarpus* (e.g. *P. dacrydioides*), in *Microcachrys* and in *Microstrobos* (=*Phaerosphera*). The leaves of the two last genera are, however, different, being small and scale-like. It is noteworthy that in one species of *Phyllocladus* (*P. glaucus*), three air bladders are sometimes found in the pollen (Cranwell 1940).

In the Jurassic of Nipania (Rajmahal Series of India), many petrified coniferous remains have been described, some belonging to the Podocarpaceae. *Nipanioruha* (as described by Rao 1946, and lately emended by Vishnu Mittre 1957) bears leaves comparable in shape with those of *Trisacocladus* and there is much more information available on the anatomy of these leaves which is lacking in our material. Male cones of the Indian genus are surrounded by leaves and therefore differ from *Trisacocladus* male cones which are shortly pedunculate and not covered by leaves. Both types of cones produce pollen with three air bladders.



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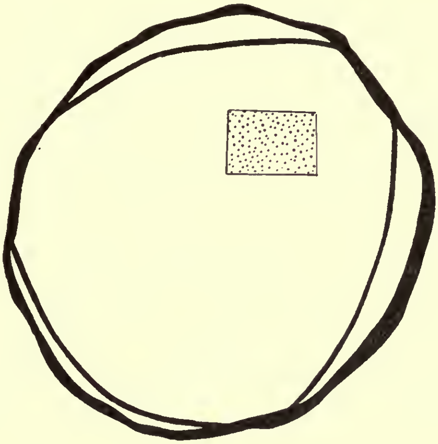

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FIG. 25. *Trisacocladus tigrensis* gen. et sp. n. Pollen grain showing three air sacs with their basal depressions. Slide LP 244, ×1100.

FIG. 26. *Apterocladus lanceolatus* gen. et sp. n. Pollen grain showing three rudimentary equatorial air bladders. Slide LP 242, ×1100.

Among fossil conifers, our female cones may be compared with *Mehtaia* Vishnu Mittre (1957), a Jurassic Podocarp from India. *Mehtaia* has erect ovules, no epimatium but small bracts. It differs, however, in its much thinner axis and in its markedly curved micropyle (straight in our material). Furthermore, the leaves of *Mehtaia* are different from those of *Trisacocladus*. All three species of *Mehtaia* have much smaller cones (the longest is 10 mm. against 20 mm. in *Trisacocladus*). Other female cones of the same formation from India differ in having inverted ovules (including those of *Nipanioruha granthia* Rao mentioned above), well developed bracts and sometimes also epimatia. As far as I am aware, there are no other similar female structures comparable with ours.

The affinity of the *Trisacocladus* cones is close to some Recent Podocarpaceae, but there are a few important differences (some probably due to lack of information about accessory structures in our material, such as the bracts). Recent Podocarpaceae have a well developed epimatium which covers the ovules to a varying degree. They also possess bracts in relation to the ovules. Our material may have bracts but no structure which could possibly suggest an epimatium. The ovules are thus naked. I believe that this structure (epimatium), if originally present, would surely have been preserved together with the ovules in at least some of the numerous specimens examined. Although this is negative evidence, it is nevertheless suggestive.

Among living Podocarpaceae those having cones with erect ovules come closer to *Trisacocladus*. *Phyllocladus* and *Microstrobos* (=*Phaerosphera*) have erect ovules but also well developed epimatia (in *Phyllocladus* there is also an aril which, however, may be considered as a secondary feature). The cones of the living genera are usually smaller and have fewer ovules. *Microstrobos* is known only from Tasmania and South-east Australia. Recent *Phyllocladus* is known from New Zealand, Tasmania, Borneo and the New Guinea area. As a fossil it has been recorded from the Tertiary of Australia and New Zealand (Cookson & Pike 1954).

All characters of *Trisacocladus* (leaves, male and female cones) have been matched separately among living representatives of the Podocarpaceae. All other conifers may be excluded from consideration as they differ in their reproductive structures. The Recent genera *Podocarpus*, *Dacrydium*, *Microstrobos*, *Phyllocladus* and *Microcachrys* share some characters with the fossil form. Female cones with erect ovules are not known in *Podocarpus*, *Dacrydium* or *Microcachrys*. Pollen grains with three air bladders, on the other hand, are unknown in *Dacrydium* and unusual in *Phyllocladus* (and most species of *Podocarpus*). Long linear leaves are known only in *Podocarpus* and *Dacrydium*. It thus appears that no Recent genus of the Podocarpaceae shares all morphological characters with *Trisacocladus*. The Patagonian plant may well belong to a new genus of the family which became extinct in the Upper Mesozoic or Lower Tertiary. The geographical distribution of these plants was at least mainly gondwanic, being present in India, Australia, New Zealand, Antarctica and South America.

This assemblage constitutes an interesting stock of morphological characters from which many modern genera of Podocarpaceae may have arisen.

These considerations support the views expressed by Florin (1963) as to the origin and distribution of the Podocarpaceae in the past. The wide gap in our knowledge of this family in the Mesozoic is only partly filled by the impressions of leafy shoots, placed in noncommital genera such as *Pagiophyllum* or *Elatocladus*. But evidence is slowly accumulating in respect of this important family which must have played an outstanding role in southern lands. Our material shows how hazardous it may be to accept the presence of a living genus in old rocks on the basis of only one part of the plant. This is certainly the case with the leaves which are related to the living genus *Podocarpus*, and which may subsequently prove to have closer relationship with other members of the family, when fertile structures become available. The same may be said regarding the dispersed pollen in sediments. While it may definitely indicate a family link, it may also lead to erroneous conclusions when generic relations are established.

Genus ***APTEROCLADUS*** nov.

DERIVATION OF NAME. *Aptero*, no wings, *cladus*, leaf.

DIAGNOSIS. As for the only species, *Apterocladus lanceolatus* sp. n.

Apterocladus lanceolatus sp. n.

(Pl. 6, figs. 40–48; Pl. 7, figs. 52, 55; Pl. 8, figs. 68–70; Text-figs. 27, 28, 34)

DIAGNOSIS. Woody plants. Lateral axis of penultimate order up to 2 mm. in diameter, bearing leafy branches at a wide angle, 8 mm. apart (seen in one specimen). Branchlets straight or slightly curved, longest seen (incomplete) 3 cm. × 1·5 mm wide (excluding leaves) or 1·7 cm. wide (including leaves). Leaves homomorphic bifacial, spirally disposed but expanded in approximately the same plane by twisting of the decurrent leaf bases. Leaves firm, coriaceous, entire and flat, straight, with one median vein, spreading 50–80°, lanceolate with acute apex, 6–8 mm. long × 1·5–2 mm. broad, maximum breadth near middle of blade, gradually tapering towards apex, abruptly contracted on base, broadly decurrent, each sheathing the axis for a distance of about 1·5–2 mm. downwards. Cuticle 2–3 μ thick. Stomata present on one cuticle, forming two bands near margins. Stomata in close bands, forming ill-defined rows, longitudinally orientated; subsidiary cells of neighbouring stomata often in contact (lateral and polar); sometimes two stomata sharing a subsidiary cell.

Epidermal cells in stomatal bands usually tending to be isodiametric, sometimes rectangular. Epidermal cells on margins and middle of lamina usually rectangular or square, forming definite files. Epidermal cells on nonstomatiferous cuticle square or rectangular, forming definite files, all about 15–25 μ wide. Anticlinal cell walls unpitted, slightly sinuous, 2 μ thick. Surface wall finely granular. No papillae or hairs seen.

Stomata typically haplocheilic, monocyclic (sometimes imperfectly dicyclic). Stomatal apparatus oval. Guard cells slightly sunken, very feebly cutinized, surrounded by typically 5–6 subsidiary cells. Subsidiary cells may or may not be differentiated into polar and lateral. When differentiated, polar subsidiary cells usually square. Subsidiary cells sometimes with thickened surface wall. Mouth of pit oval or rectangular, with marked rim of cutin formed by fusion of subsidiary cells. Subsidiary cells sometimes with strong external cutin ridge parallel to mouth of pit, which may fuse with neighbouring thickening of adjacent subsidiary cells, forming a sort of ring. Hypodermis not cutinized.

Male cones shortly pedunculate, laterally attached to branches, oval, 0·6 × 0·35–0·5 cm. wide, with microsporophylls spirally inserted in central axis, close together, composed of main branch and distal (outer) leafy rhomboidal and acuminate head. More than one pollen sac present on each sporophyll.

Pollen grains sometimes with three rudimentary air bladders, almost spherical, sometimes a little flattened in polar axis. Equatorial diameter about 45 μ and polar diameter (flattened specimens) about 37 μ. Exine delicate, finely granular in texture and thinner on one half.

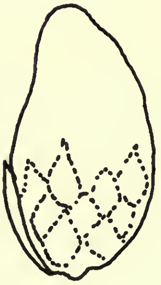
HOLOTYPE. LP 6296 (Bajo Grande, *Araucarites* bed).

MATERIAL. In addition to the holotype, LP 5665, 5666, 5698–5700, 5730, 5749 (Bajo Tigre, *Ptilophyllum* bed); LP 6302–6306, 6317–6327; BMNH, V.52282–93 (Bajo Grande, *Araucarites* bed). Slides LP 228–230, 242, 243, 245, 246; BMNH, V.52294–95 (Bajo Grande, *Araucarites* bed).

HORIZON AND LOCALITY. Lower Cretaceous, Baqueró Formation, lower member, Bajo Grande, *Araucarites* bed and Bajo Tigre, *Ptilophyllum* bed, Santa Cruz Province, Argentina.

DESCRIPTION. *Apterocladus lanceolatus* is common in Bajo Grande, and occurs in the same bed as the other conifers *Araucarites minimus, Podocarpus dubius* and *Tomaxellia biforme.* Its preservation is similar, although the cuticle is not easy to prepare. The leaf is coaly and broken into small fragments which cannot be pulled out together. The largest fragments were treated with dilute alkali and then bits of cuticle were separated. However, the cuticle usually adheres very strongly to the rock matrix and better results were obtained by first dissolving the matrix with HF to free the cuticles. In both cases the cuticle appears very fragmentary but shows some diagnostic characters. One specimen (LP 6296) shows clearly a male cone in organic attachment to a leafy shoot. Pollen was obtained by scraping the organic remains on the microsporophylls. All grains are of one kind. Similar isolated male cones are abundant in the same bed. They all possess the same type of pollen grains and have therefore been included in the species. One of the isolated male cones (LP 6323) has a few compressed scale leaves at the base which after treatment with dilute alkali, showed very small fragments of cuticle with elongated epidermal cells. These cuticular fragments are similar to the leaf cuticle of *Apterocladus lanceolatus.* The cones are single or may be present in pairs (LP 6321, BMNH, V.52293).

Apterocladus lanceolatus also occurs abundantly in Bajo Tigre, in the *Ptilophyllum* bed (named here for the first time). These specimens lack a cuticle, but are otherwise identical. Only the impressions of square and rectangular epidermal cells can be seen, arranged in definite longitudinal files. Fragmentary remains, possibly belonging to this species were found in the Ticó Amphitheatre. (*Otozamites grandis* bed, LP 5149 and *Ticoa harrisii* bed LP 5370). One specimen yielded cuticle fragments with square or rectangular epidermal cells, arranged in files. One other speci-



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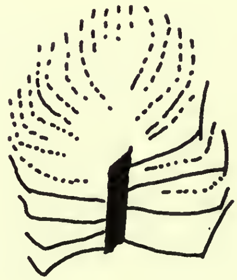

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FIGS. 27, 28. *Apterocladus lanceolatus* gen. et sp. n. Fig. 27. Male cone showing impressions of the outside of some microsporophylls and one leaf near base. BMNH. no. V.52291, ×8. Fig. 28. Male cone showing central axis and insertion of a few microsporophylls. LP 6326, ×8.

men from the *Taeniopteris* bed (LP 5279) shows a few leaves more than 1 cm. long, with tapering base and apex, one vein, but no cuticle is preserved. These fragments suggest that *A. lanceolatus* may be of widespread occurrence (it is over 50 km. from Ticó to Bajo Grande).

The pollen grains are interesting in that they have a clear equatorial thickening which is sometimes trilobed. These lobes may well represent incipient air sacs, in which case there is further evidence for including *Apterocladus* in the Podocarpaceae. Many similar pollen grains found detached in the sediments show this character. A detailed study of the pollen grains has been published by Gamerro (1965).

Discussion. *Apterocladus lanceolatus* differs from all other conifers so far studied in the Ticó flora. The leaves are only comparable to *Podocarpus dubius* although there are many differences in shape and in cuticular structure. Stomata of both species are placed in bands, always longitudinally orientated, with oval or rectangular mouth of pit. These characters definitely indicate a Podocarpaceous affinity. Some Taxodiaceae have leaves of similar habit, but usually they are amphistomatic. Moreover, the orientation of stomata in Taxodiaceae is irregular (they may be longitudinally, obliquely or transversely orientated). Only *Sequoia*, *Taxodium* and *Glyptostrobus* have leaves of similar habit to *Apterocladus*.

The pollen grains of *A. lanceolatus* differ from those of Taxodiaceae in the lack of a papilla-like germinating pore. In this respect they are more like those of Recent Araucariaceae, although presenting some differences in the structure of the exine. Most Recent Podocarpaceae have markedly winged pollen grains, and therefore differ from our species. Only *Saxegothaea* resembles our species in having wingless grains, but the exine structure is rather different and the size of the grains is smaller in the Recent genus. The vegetative part of *Saxegothaea* also bears some resemblance to our fossil. The leaves are, however, much longer (although contracted at the base) while the male cones are shorter than those of *Apterocladus*. The cuticular structure is similar in that *Saxegothaea* bears stomata on one epidermis, placed in two bands and longitudinally orientated. However, in the Recent genus the stomatal rows are better defined than in *Apterocladus*. Finally, epidermal cells in the Recent genus although rectangular and placed in files, have markedly sinuous walls, a character lacking in *Apterocladus*. Nevertheless, *Apterocladus* appears to be more closely related to *Saxegothaea* than to any other living conifer. This genus is now known in the Patagonian Andes (Chile and Argentina), not far from where the Baqueró Formation is exposed (less than 500 km.). It may be worth mentioning that *Saxegothaea* has been recorded from the Oligocene of Fueguia (about 700 km. southwards), although there is some doubt about Dusen's determination (1899).

The pollen grains of *Apterocladus* may well be compared (or confused) with some *Araucaricites* found in dispersed condition. Its grains have the equatorial thickened zone which might represent incipient sacci, and the thinner exine of one of the halves might represent a colpus. Thus a winged grain may be derived from *Apterocladus*, such as the grains of *Phyllocladus*, some of which have very small incipient sacs. On the other hand, the incipient sacci could represent a step in a reductionary series, in which case the next step would be represented by non-saccate grains (as in *Saxegothaea*).

The contracted leaf bases of *Apterocladus* distinguish it from all the species of *Elatocladus* described by Halle (1913*a*) from the Jurassic of Graham Land. There may be some resemblance to *Elatocladus* sp. figured by Halle (1913, pl. 5, fig. 8) from the Lower Cretaceous of Rio de los Fosiles, Santa Cruz ; but here the contraction at the base of the leaves is gradual, while it is more marked in *Apterocladus*.

Coronelia molinae Florin (1940), from the Tertiary of Chile shares with *Apterocladus* the character of contracted leaf-bases, although in the Chilean species this constriction is much more pronounced. There are also differences in cuticular structure, mainly in the presence of papillae and peculiar hairs in *C. molinae*.

There is some resemblance to the two species of *Palissya* described by Frenguelli (1949) from the Upper Jurassic of Chubut Province, Argentina. The leaves are similar and have contracted bases, but nothing is known about their cuticular structure.

Genus ***PODOCARPUS*** L'Héritier

Podocarpus dubius sp. n.

(Pl. 6, figs. 49, 50 ; Pl. 7, figs. 53, 54 ; Text-figs. 29–33)

DIAGNOSIS. Woody plants. Lateral axis of penultimate order up to 3·5 mm. in diameter, bearing leafy branchlets at an angle of about 45°, 1–1·5 cm. apart (in a row). Branchlets usually straight, sometimes slightly curved, longest seen (incomplete) 4 cm. × 2 mm. (not including leaves) or 2 cm. wide (including leaves). Leaves dimorphic. Large leaves usually of bilateral type, spirally disposed, linear, straight or falcate, spreading (40–80°), tapering to acute or acuminate apex, with uncontracted, markedly decurrent base, sheathing axis for about 4–5 mm., uninerved, largest 1·3 cm. × 1·5 mm. broad in free portion. Short leaves usually situated at base of branchlets or near apex, or on branches of penultimate order ; they are spirally disposed, adpressed to axis or spreading in all directions, markedly decurrent (decurrent sector sometimes larger than free part of leaf). Short leaves may occasionally be placed among long leaves. Both cuticles of same thickness, about 3–4 μ. Stomata present on both cuticles, few on decurrent sector and forming ill-defined rows. In middle sector of leaf, stomata placed in two well defined bands per epidermis, tending to be near margins leaving a conspicuous median sector devoid of stomata (this sector may correspond to real lateral margins of the leaf). Stomata in bands, forming more or less defined longitudinal rows, longitudinally orientated, sometimes obliquely, never transversely. Stomata of a row sometimes with subsidiary cells in contact, but never shared.

Epidermal cells in stomatal bands isodiametric or elongated, with rounded contours. Square or rectangular epidermal cells on same rows as stomata. Those on margins and middle of lamina typically rectangular, about 20 μ wide, placed in files. Median longitudinal sector sometimes occupied by markedly elongated rectangular cells. Cell walls straight, unpitted, 3–4 μ thick, with finely granular surface. Round delicate papillae, occupying most of cell surface, sometimes seen.

Stomata haplocheilic, monocyclic to imperfectly dicyclic. Stomatal apparatus oval. Guard cells slightly sunken, very feebly cutinized, surrounded by typically 4–5 subsidiary cells. Subsidiary cells occasionally with cutin ridges parallel to mouth of pit. Polar subsidiary cells sometimes differentiated, when differentiated usually square. Mouth of pit oval, sometimes rectangular, constricted by a strong rim of cutin formed by fusion of subsidiary cells. Rim of cutin of stomata less conspicuous in one of the two cuticles. Hypodermis not cutinized.

HOLOTYPE. LP 6309.

MATERIAL. In addition to the holotype, LP 6307–13, 6414–29 ; LIL 2753–62 ; BMNH, V.52296–99. Slides V.52300–01 ; LP 221–227.

HORIZON AND LOCALITY. Lower Cretaceous, Baqueró Formation, lower member, *Araucarites* bed. Estancia Bajo Grande, Santa Cruz Province.

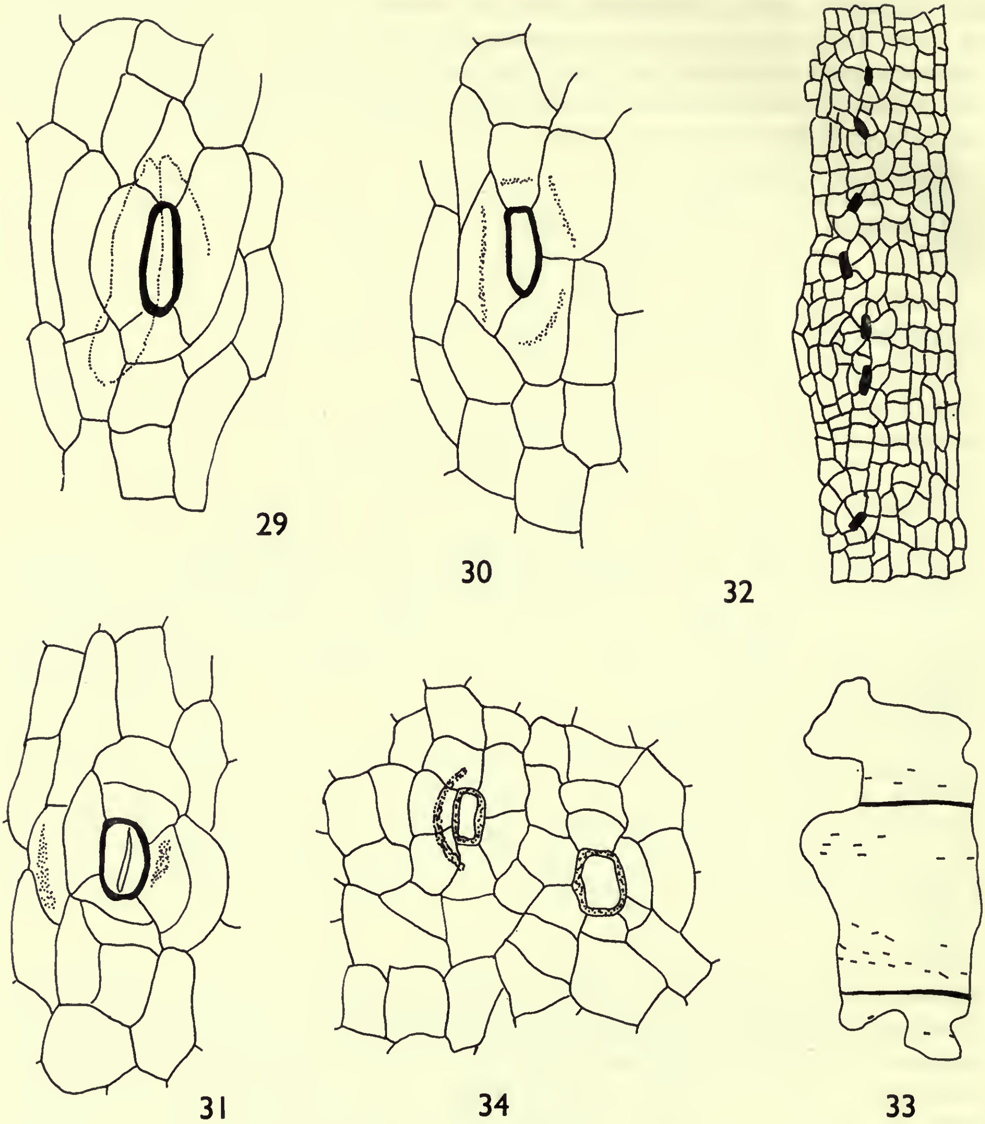
DESCRIPTION. This is one of the commonest species in the *Araucarites* bed of the Bajo Grande locality. The substance of the leaves is coaly and broken into small fragments which can be treated with dilute alkali in order to obtain small bits of cuticle. The leaves of most specimens examined are usually of the long type, and in one rank of a branchlet their length may vary considerably. Short leaves were seen in a few specimens ; they usually occur at the base of branches. Unfortunately it was impossible to obtain cuticular fragments from these small leaves. Long leaves are considered to be of the bilateral type because there is no evidence of torsion at the base and yet they tend to be disposed in one plane. The base of these leaves is wide and they sheath the axis for a considerable distance. Following Laubenfels's classification of coniferous leaves (1953) they fall into his type I, tetragonal in cross-section and falcate in profile.

Stomatal bands are clearly defined. Although only small portions of cuticle were obtained I believe that there are more stomata in the bands of the lower cuticle, especially on the unexposed surface. Text-fig. 33 shows a sector of a long leaf. The two black lines may correspond to a keel and thus the stomatal bands between these lines correspond one to half the lower cuticle and the other to half the upper cuticle.

DISCUSSION. This species differs clearly from all conifers so far studied in the Ticó flora. *Tomaxellia degiustoi* is the one which comes closest, but it differs in leaf arrangement (radially disposed and not spreading in one plane). Also the cuticular structure is different ; in *Tomaxellia* stomatal bands have no definite stomatal rows.

There is some resemblance to *Elatocladus conferta* (Oldham) from the Jurassic of Hope Bay (Halle 1913*a*), although the leaves of *Podocarpus dubius* sp. n. are usually longer. Florin (1940 : 31) considers *E. conferta* to be similar to Recent *Podocarpus* of the *Eupodocarpus* section. *Elatocladus jabalpurensis* (Feistm.) and *Elatocladus* sp. (Halle 1915*a*, pl. 9, figs. 7–9) may also be compared with our species. Florin (1940) considers these two species as *Podocarpus*, subgenus *Stachycarpus*.

Frenguelli (1949) described some fertile specimens of probable Jurassic age from the Canadón Asfalto, near Paso de los Indios in the Chubut Province. These plants



FIGS. 29–33. *Podocarpus dubius* sp. n. Figs. 29–31. Stomata. (Fig. 29, slide LP 225. Fig. 30, slide LP 226, Fig. 31, slide LP 221). All ×370. Fig. 32. A stomatiferous row on lower cuticle. Slide LP 225, ×85. Fig. 33. Disposition and orientation of stomata on a bilateral leaf (upper half, probably upper cuticle). Slide LP 226, ×30.

FIG. 34. *Apterocladus lanceolatus* gen. et sp. n. Two stomata. Slide LP 228, ×370.

were referred to *Palissya conferta* (Oldham) and *Palissya jabalpurensis* Feistm. Both species differ from ours in their contracted leaf bases. The female cones, judging from Frenguelli's illustrations (1949, pls. 1, 2) are rather obscure structures. His reconstruction of the cone scales (text-fig. 1) is tentative and must be critically considered. All previous references of *Palissya* from India have been discarded. Most of the species have been included in the artificial genus *Elatocladus* in order to differentiate them from typical species of *Palissya* better known from shoots and female cones in Europe (Florin 1963). This *status* should be accepted until better material of the Gondwana floras becomes available. Frenguelli's specimens would be better placed in the genus *Elatocladus*.

Podocarpus? palissyafolia (Berry) Florin from the Baqueró Formation in Cerro Cuadrado and Punta del Barco was originally described as *Elatocladus palissyafolia*, on the basis of a fragmentary specimen (Berry 1924). It differs from *Podocarpus dubius* in the contracted leaf bases but is similar in other respects. The leaves are not bilateral as in our species. Unfortunately, this material is too fragmentary for exact identification and no new material is available from the type localities.

Podocarpus inopinatus Florin, from the Tertiary of Chile, has similar but smaller leaves (4–7 mm. long against up to 1·3 cm. long in our species). There is general agreement in cuticular structure: the leaves are amphistomatic, with marginal bands of stomata and epidermal cells arranged in rows. However, in *P. inopinatus* neighbouring stomata may share a polar subsidiary cell, but this has not been observed in our material. Moreover the Chilean species has dicyclic stomata while *P. dubius* has monocyclic to imperfectly dicyclic stomata. Pitting of the anticlinal cell walls reported for the Chilean species is unknown in our material. *Podocarpus inopinatus* belongs to the section *Dacrycarpus* of the genus (according to Florin). The other two species of *Podocarpus* described by Florin in the same paper differ in the shape and insertion of their leaves, and in cuticular structure.

Among the Indian species of *Elatocladus*, there are two with bilateral leaves similar to those of *P. dubius*. In *E. plana* (Feistmantel 1879, Seward 1919, text-fig. 802, Sahni 1928) the leaves are much longer and disposed closer to each other. *E. tenerrima* (Feistmantel 1877, Sahni 1928) differs in the typically wide angle of insertions of leaves (almost perpendicular to the branches); in *P. dubius*, the leaves normally form an acute angle with the branch. Both Indian species may, however, be closely related to *P. dubius* in having bilateral and amphistomatic leaves.

So far as comparison with living conifers is concerned, *Podocarpus dubius*, having bilateral leaves may be closely compared with the Podocarpaceae. Among the family, this condition is known to occur in the genera *Acmopyle*, *Dacrydium* and *Podocarpus* sect. *Dacrycarpus*. I believe that our species in leaf morphology and cuticular structure is better placed in *Podocarpus*. Lacking other characters, this combination is to be preferred (following Florin's (1940) paper on Tertiary material from Chile). The difference in age is, however, considerable and I am not sure that our species really belongs to *Podocarpus* as we know it from Recent material.

The main difference between *Podocarpus dubius* and other genera with similarly shaped leaves is the bilateral condition of the leaves in *P. dubius*, not found in any other families except the Podocarpaceae. The arrangement of stomata in bands is a common character in both Podocarpaceae and Taxodiaceae, but in the former, more or less well defined files of stomata occur in bands as they do in *P. dubius*. On the other hand all living Taxodiaceae are exclusive to the Northern Hemisphere, with the exception of *Athrotaxis*, which is clearly different from our species and is known living and fossil from the Southern Hemisphere. Among Araucariaceae there are no similar species, all possess leaves of one kind (with no foliar dimorphism).

Podocarpus dubius may be considered as another fossil member of the Podocarpaceae which inhabited Patagonia during Lower Cretaceous times.

Genus ***TOMAXELLIA*** Archangelsky 1963 : 86

EMENDED DIAGNOSIS. Woody plants with branches up to the fourth order. Leaves decurrent, spirally inserted, homomorphic (long) or dimorphic (long and short). Long leaves narrow, ending with acute apex, widest at their decurrent part, rhomboidal in transverse section, with sharp lateral angles.

Cuticle thick. Stomata present on both cuticles. On lower cuticle, at base of leaves stomata irregularly distributed and indistinctly orientated ; stomata forming irregular bands in middle of lamina. On upper cuticle stomata usually forming two bands from base to near apex. Orientation of stomata on free part of both cuticles oblique to longitudinal, sometimes transverse. Rows of stomata in bands ill-defined. Stomata when in a row usually separated, sometimes with outer encircling cells in contact, never sharing subsidiary cells. Epidermal cells between stomatal bands, rows and margins elongated, rectangular.

Stomata similar on both cuticles, monocyclic to dicyclic. Stomatal apparatus oval or circular (never rectangular). Guard cells sunken in a pit, surrounded by typically 4–5 subsidiary cells. Hypodermal cells cutinized, markedly elongated.

DISCUSSION. Only one species of *Tomaxellia* (*T. degiustoi*) has so far been described (Archangelsky 1963). New material from Bajo Grande includes a new species, *T. biforme*, and this together with additional specimens from the type locality in Ticó Amphitheatre are described below Comparisons have already been made with Recent genera of Araucariaceae, Taxodiaceae and Podocarpaceae, and with the fossil genera *Elatides* and *Elatocladus*.

Vishnu-Mittre (1957) described a new genus, *Indophyllum* for shoots having leaves with free margins of lamina extending beyond the leaf cushion (as in *Pagiophyllum*) but they are homomorphic and much shorter than in *Tomaxellia*. One of his three species, *Indophyllum raoi*, has leaves which are rhomboidal in cross-section. In all three species, the stomata are longitudinally orientated. Only in *I. raoi*, on the lower cuticle, are the stomata irregularly orientated but they are longitudinally orientated on the upper epidermis and therefore differ from *Tomaxellia*. No detailed comparison of the stomatal structure is possible, because many characters are not preserved in the Indian material. *Indophyllum* is of Upper Jurassic age. Other leaves described from the same formation differ in having definite Podocarpaceous characters such as orientation of stomata in bands and stomatal structure.

Tomaxellia degiustoi Archangelsky

(Pl. 4, fig. 17)

1963 *Tomaxellia degiustoi* Archangelsky : 87, pl. 7, figs. 39, 40 ; pl. 8, figs. 58–60 ; pl. 11 ; pl. 12, fig. 79 ; text-figs. 72–74.

The new material collected in 1962 from the *Ticoa harrisii* bed in the Ticó Amphitheatre, yielded some good fragments of this species. When originally described, *T. degiustoi* was based on two very small fragments of branchlets and isolated leaves found in the rock matrix. With these new specimens knowledge of the gross morphology of branches and branchlets is now available. The leaves are spirally disposed on the branches and do not spread in one plane, as they do in many of the Podocarpaceae. The angle formed by the leaves with the axis is always very acute (never more than 45°), usually about 20–30°. Sometimes the leaves are almost adpressed to the axis. The broadest branches seen show clearly the oval scars of the leaf cushions. The branchlets are irregularly disposed on the branches, and may be widely separated or almost opposite. The cuticles are identical with those of typical material.

The original diagnosis has been enlarged in respect of the external morphology, the rest has been left unchanged.

Emended diagnosis. Woody plants. Branches straight or slightly curved, 3 mm. in diameter, longest seen 11 cm. (base and apex truncated) bearing irregularly inserted branchlets at distances varying from 1–3·5 cm. Branchlets forming acute angle with branch (about 10–50), straight or slightly curved, 4–5 cm. long (incomplete) bearing homomorphic leaves spirally inserted and spreading at acute angle or tending to be adpressed to axis. Leaves falcate, long and narrow, slightly decurrent, almost acicular, up to 1·3 cm. long × 1·5 mm. wide, ending with acute apex. Leaves broadest at base, gradually tapering towards apex. Leaf cushion on branches large, persistent, up to 8 mm. long × 2·5 mm. broad. Leaf cushions on branchlets small, oval or rhomboidal, 2 mm. long × 1 mm. broad. Free part of leaf rhomboidal in transverse section, but upper and lower angles somewhat rounded ; in middle region of leaf lower angle bearing wide short papillae. Lateral angles sharp, entire.

Cuticle as for original diagnosis.

Material. In addition to the material quoted in 1963 ; LP 5052, 5059, 5117, 5342.

Horizon and locality. Lower Cretaceous, Baqueró Formation, lower member, *Ticoa harrisii* bed. Estancia La Magdalena, Ticó Amphitheatre, Santa Cruz Province, Argentina.

Tomaxellia biforme sp. n.

(Pl. 4, figs. 18–20 ; Pl. 7, fig. 51 ; Text-figs. 35–39)

Diagnosis. Main branches 3 mm. wide, giving off in different planes numerous lateral branchlets of a second order, up to 6 cm. long ; these branches give off at acute angle lateral shoots of a third order, which may branch once again to give branchlets of ultimate order. Leaf cushions small, oval or rhomboidal, about 1·5 mm. long × 1 mm. broad. Leaves spirally disposed, mainly of two kinds: (1) short, with rounded apex and adpressed to axis, and (2) long, linear, with acute apex, with free part spreading outwards at almost right angles. Longest leaf, 4·7 mm. × 2 mm. wide; shortest, 1·5 mm. × 0·8 mm. wide. Length-breadth ratio from 4·3 : 1 to 1·6 : 1. Leaves widest at their decurrent part (on leaf base cushion). Apex of leaves may project towards the stem. Leaves in section probably rhomboidal, with sharpened lateral angles and rounded lower angle; upper angle not prominent. Veins not seen.

Cuticle 4–5 μ thick. Stomata present on both cuticles. On lower cuticle, at base (decurrent sector) stomata irregularly distributed and variably orientated; in middle of lamina forming two irregular bands near lower angle which becomes thinner towards apex. Stomata on upper cuticle forming two bands from base towards apex, leaving clearly two marginal and one central sector devoid of stomata. Orientation of stomata on both cuticles tending to be oblique or longitudinal. Two marginal sectors, 10–15 cells wide, devoid of stomata and clearly marked on lower cuticle. On both cuticles, rows of stomata in stomatal bands may be present; usually not well defined. Stomata present near apex on both cuticles. Stomata when in a row, usually separated, sometimes with outer encircling cells in contact, but never sharing subsidiary cells. Epidermal cells on base (decurrent sector) about 30–35 μ in diameter, isodiametric (square or with rounded contours). Epidermal cells in stomatal bands isodiametric or rectangular (longitudinally or transversely orientated). Epidermal cells towards margins becoming more rectangular, longitudinally orientated, up to more than 100 μ long. On margins, where both cuticles join, epidermal cells project outwards, forming a serrate edge with free apices of cells, this character being more prominent in smaller leaves, and almost non-existent in larger leaves. Cell surface flat, with no trichomes or papillae, sometimes faintly granular. Anticlinal walls straight, unpitted, strongly cutinized down to hypodermis, about 5 μ thick.

Stomata similar on both cuticles, typically imperfectly monocyclic to dicyclic. Stomatal apparatus usually oval or circular (never rectangular). Guard cells sunken in a pit, very feebly cutinized, surrounded by typically 4–5 inner subsidiary cells more or less isodiametric, finely striated, forming mouth of pit, slightly sunken below general epidermal surface. Outer encircling cells strongly cutinized with inner lateral walls slightly overhanging depression of the epistomatal chamber.

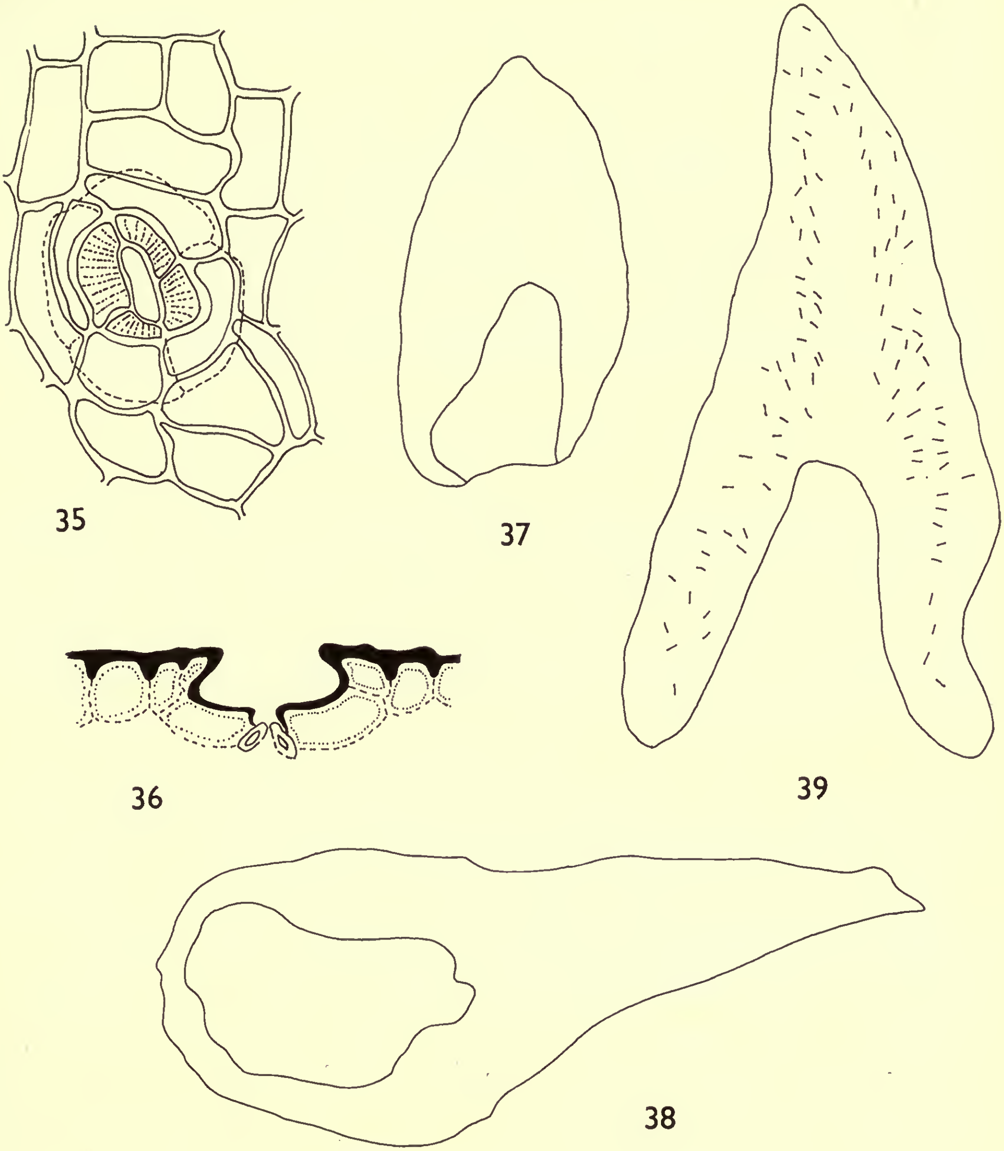
Hypodermal cells cutinized, markedly elongated.

HOLOTYPE. LP 6278.

MATERIAL. In addition to the holotype, LP 6279–80, 6283–87, 6289–93, 6297; BMNH, V.52279–82. Slides LP 199–218; BMNH, V.52283–86.

HORIZON AND LOCALITY. Lower Cretaceous, Baqueró Formation, lower member, *Araucarites* bed; Estancia Bajo Grande, Santa Cruz Province, Argentina.

DESCRIPTION. This is a very common species in the *Araucarites* bed of Bajo



Figs. 35–39. *Tomaxellia biforme* sp. n. Fig. 35. Stoma. Slide LP 202, ×370. Fig. 36. Section of a stoma, ×370. Fig. 37. A short leaf. Slide LP 200, ×30. Fig. 38. A long (normal) leaf. Slide LP 199, ×30. Fig. 39. Distribution and orientation of stomata on upper epidermis. Slide LP 202, ×30.

Grande. The leaves are usually of the long type, but short leaves are not uncommon ; this short type may occur singly or in groups or series, followed by series of longer leaves. This dimorphism is known to occur among both fossil and Recent conifers. There is great variation among the leaves of this species, but they are alike in cuticular structure, and in stomata in particular. The distribution of stomata on the upper epidermis is characteristic ; at the base of the leaf they tend to be transversely orientated. On the lower cuticle, stomata may be present directly on the lower angle or else there may be a zone devoid of stomata. Epidermal cells are usually devoid of papillae, but in one specimen (LP 6286) several leaves showed papilla-like cutin thickenings on the apical sector of the lower cuticle, occurring on the transverse anticlinal walls of rectangular cells. Also in these specimens, the lateral serrate margins are more conspicuous than in other forms of the species, but this is a varying character. Stomatal apparatus is alike in all specimens examined. Sometimes 6 subsidiary cells are present, but usually there are 4–5. The striation of inner subsidiary cells is constant, and the striae tend to be placed transversely to the mouth of the pit.

ACKNOWLEDGMENTS

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PLATE 1

Pachypteris elegans sp. n.

FIG. 1. General aspect of holotype. LP 6233, ×1.

Ticoa lamellata sp. n.

FIG. 2. General aspect of holotype. LP 6250, ×1·3.

FIG. 8. Lower cuticle (middle) and upper cuticle (right). Slide LP 174, ×30.

FIG. 9. Lower cuticle showing distribution of stomata and small hair bases. Slide LP 174, ×100.

Almargemia incrassata sp. n.

FIG. 3. Fragmentary pinnae. Left, BMNH, no. V.52664; right, LP 6254, ×1·3.

FIG. 4. General aspect of holotype. LP 6255, ×1·3.

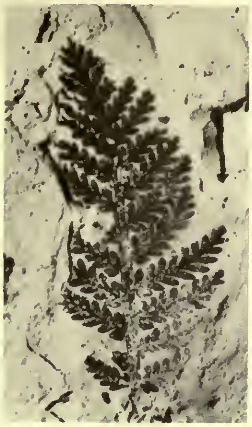
Araucarites baqueroensis sp. n.

FIG. 5. General aspect of holotype. LP 5766*b*, ×1.

Araucarites minimus sp. n.

FIG. 6. General aspect of holotype. LP 6329, ×3.

FIG. 7. A small scale showing acuminate apex. LP 6330, ×3.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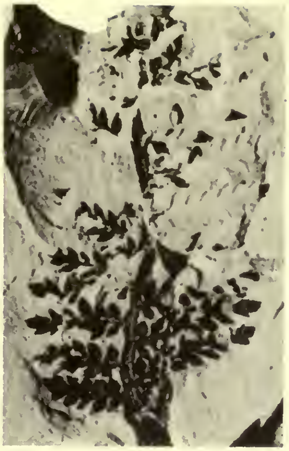
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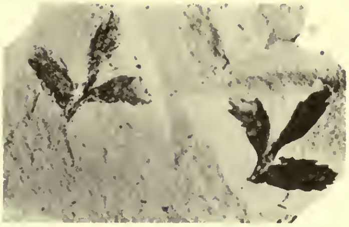
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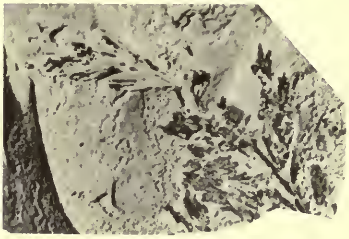
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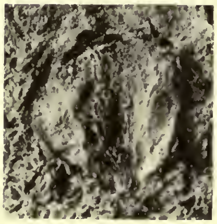
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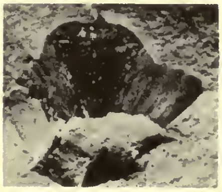
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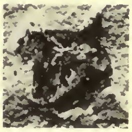
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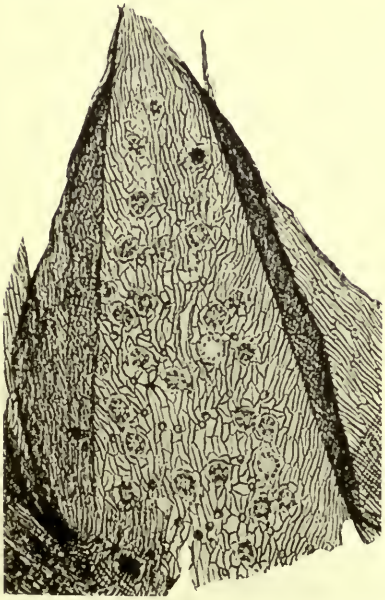
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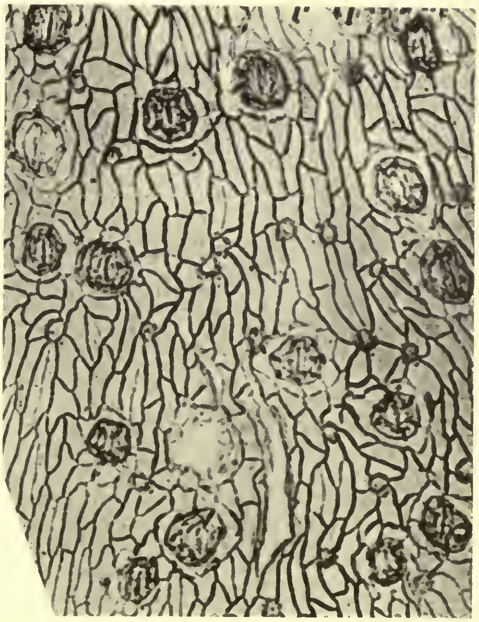
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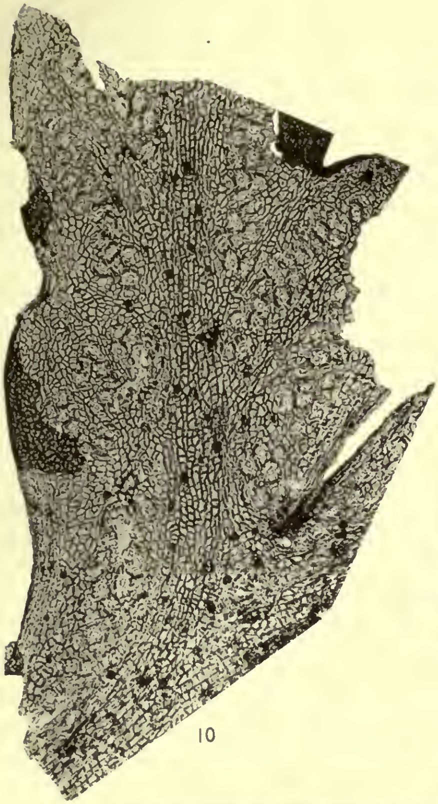
PLATE 2

Pachypteris elegans sp. n.

FIG. 10. Lower cuticle of undifferentiated pinna, showing distribution of stomata and venation. Slide LP 169, ×30.

FIG. 11. Lower and upper cuticles of a pinnule. Slide LP 170, ×30.

FIG. 12. Stomata on lower cuticle. Slide LP 169, ×500.



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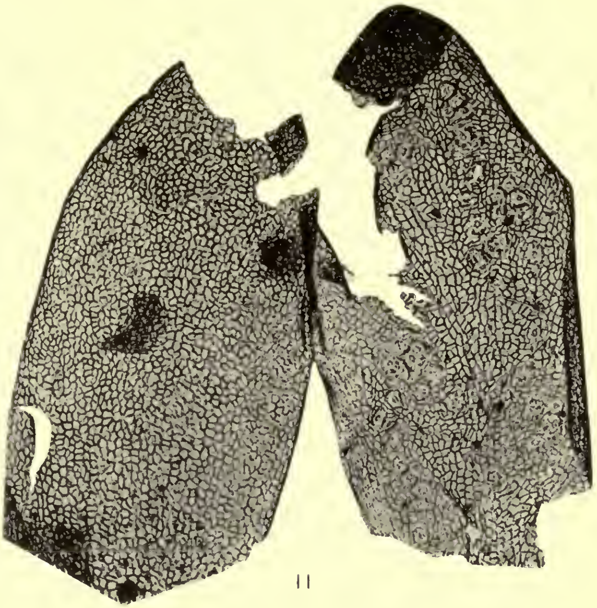

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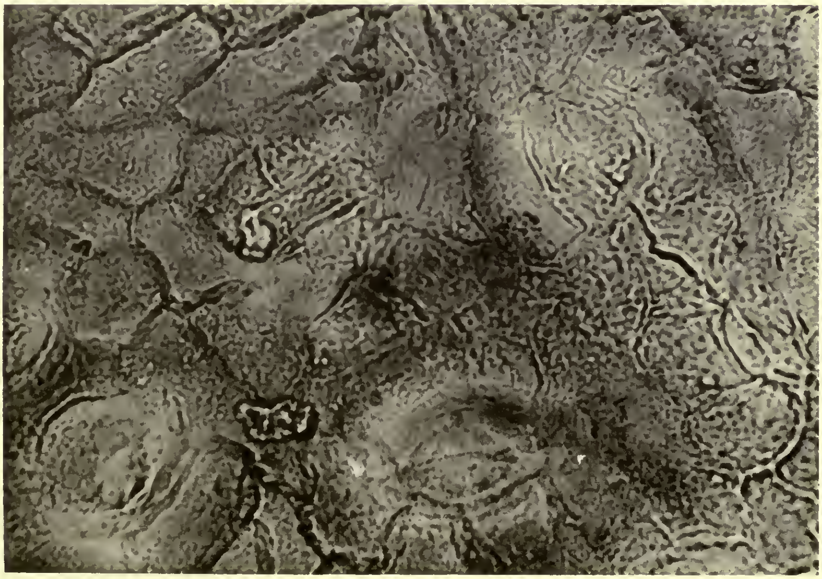

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PLATE 3

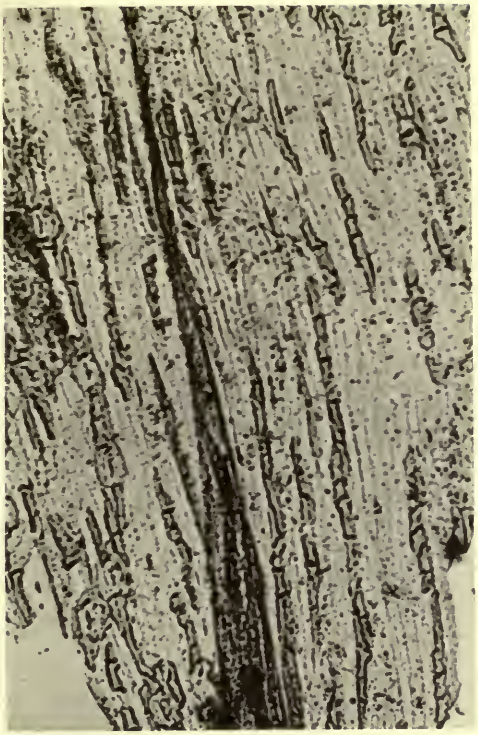
Almargemia incrassata sp. n.

Fig. 13. Lower cuticle (left) and upper cuticle (right) showing two types of epidermal cells. Slide LP 184, ×100.

Fig. 14. Lower cuticle showing stomata. Slide LP 184, ×500.

Ticoa lamellata sp. n.

Figs. 15, 16. Stoma focused at two different levels. 15, mouth of pit; 16, guard cells. Slide LP 174, ×500.



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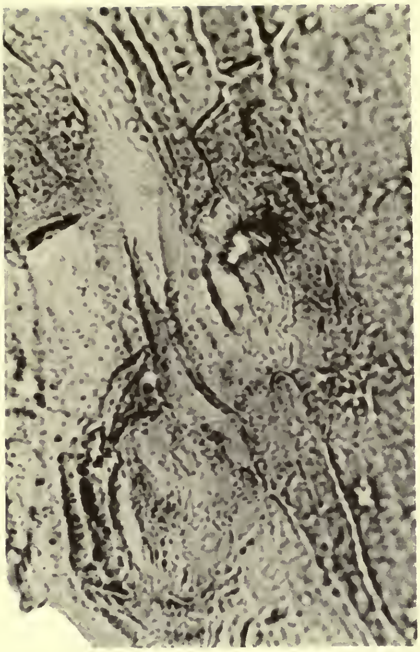

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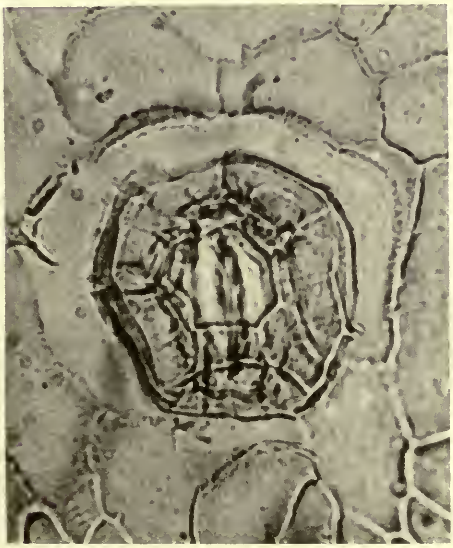

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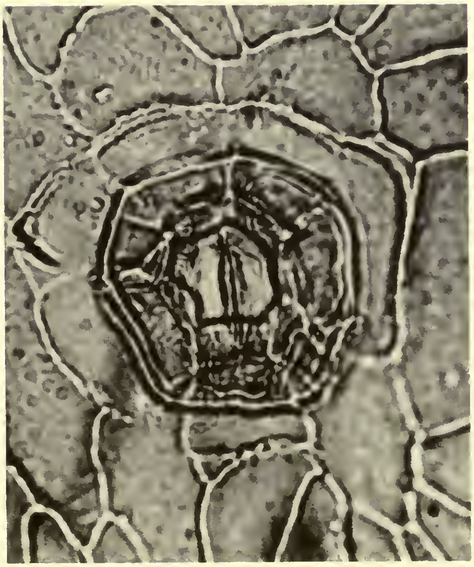

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PLATE 4

Tomaxellia degiustoi Archangelsky

FIG. 17. Branched specimen. LP 5117, ×1·3.

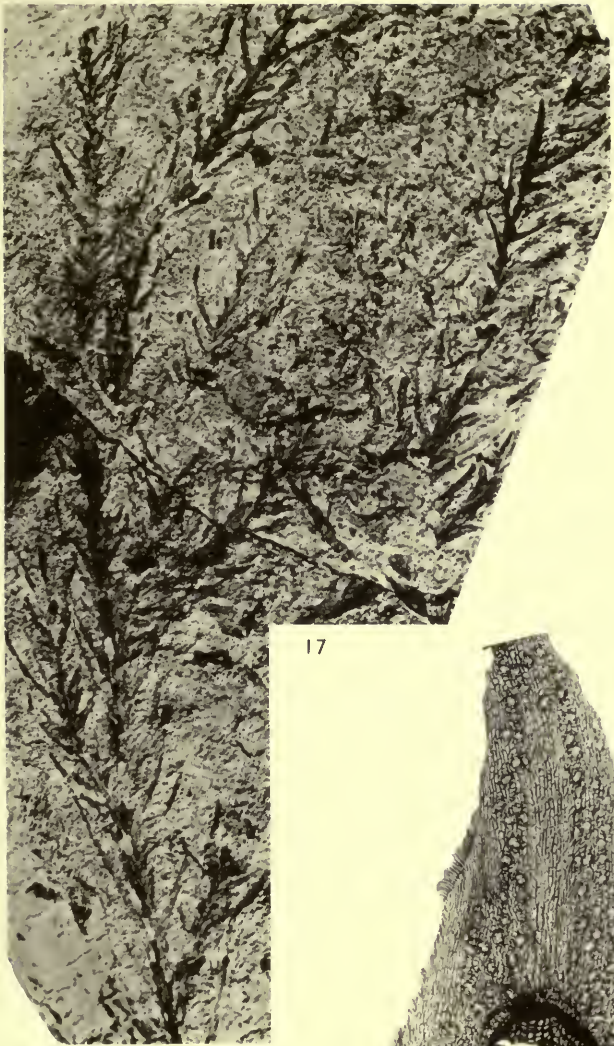
Tomaxellia biforme sp. n.

FIG. 18. General aspect of holotype. LP 6278, ×0·75.

FIGS. 19, 20. Lower (19) and upper (20) cuticles, showing distribution of stomata. Slide LP 202, ×30.

Trisacocladus tigrensis gen. et sp. n.

FIG. 21. Two fragmentary branches. LP 5845, ×1.



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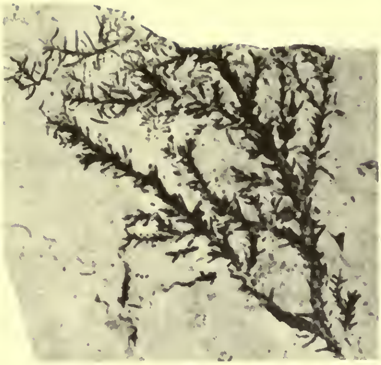

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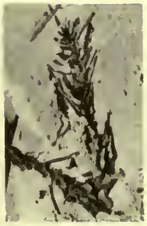

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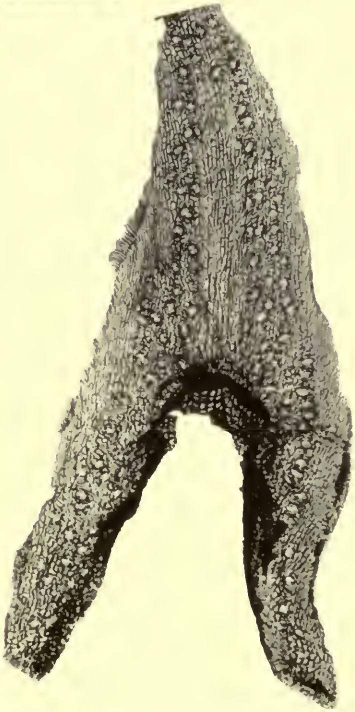

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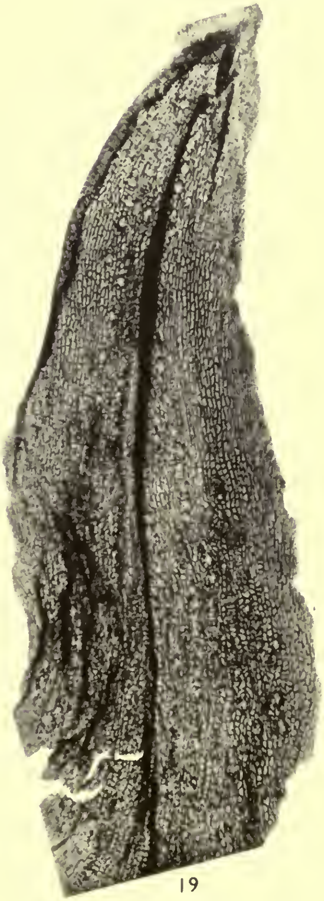

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PLATE 5

Trisacocladus tigrensis gen. et sp. n.

FIG. 22. Same specimen as Fig. 21, ×3.

FIG. 23. Branched twig with leaves spreading in one plane. LP 5827, ×1·5.

FIG. 24. Holotype. Pollen sacs are seen as paler structures among microsporophylls. LP 5826, ×1·5.

FIG. 25. The same, ×4.

FIGS. 26–28. Male cone, three different magnifications, showing microsporophylls. LP 5829, ×1, ×3, ×8.

FIGS. 29, 30. Wide branch showing leaf scars. BMNH. no. V.52238, ×1 and ×3.

FIGS. 31, 32. Branch with female cone, showing probable attachment. LP 5846. Fig. 31, ×1 and Fig. 32, ×3. *ca*, cone axis; *o*, ovules still attached to cone axis.

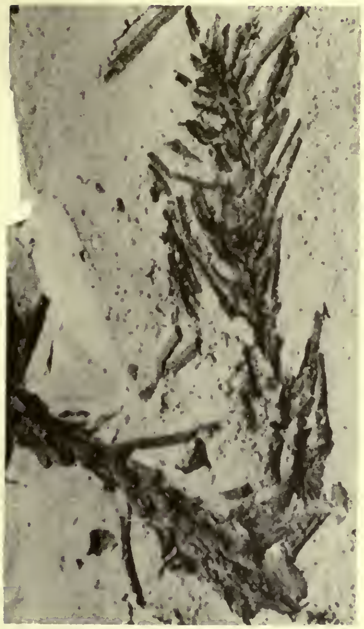
FIG. 33. A detached seed. LP 5847, ×10.

FIG. 34. A cone axis showing irregular scars. LP 5842, ×1.

FIGS. 35–37. Cone showing axis and a few ovules laterally attached. LP 5838, ×1 and ×3; counterpart LP 6231, ×2. The white dots are remnants of megaspores.

FIG. 38. Cone axis and attached ovules. LP 6218, ×2.

FIG. 39. Cone axis with probable bracts (?) transversely disposed. LP 6215, ×2.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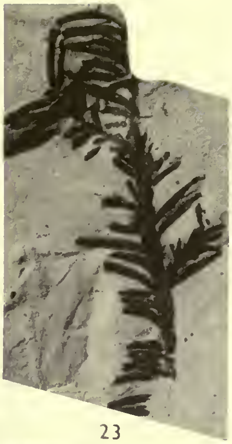
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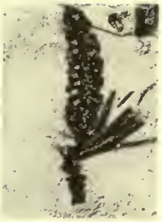
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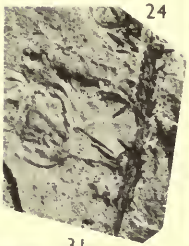
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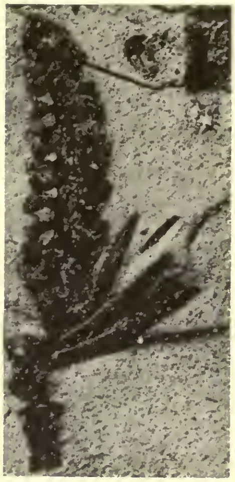
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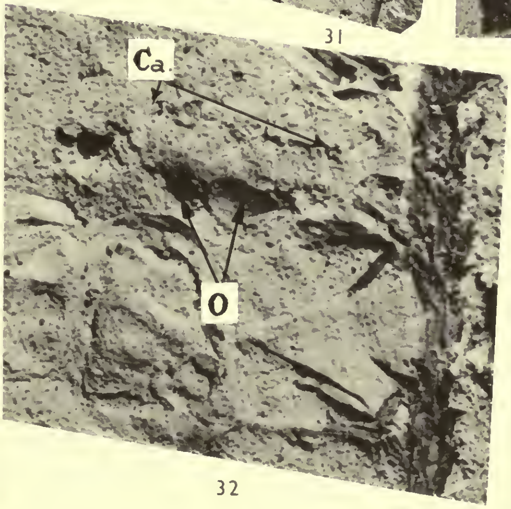

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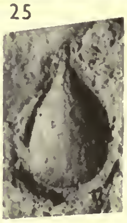
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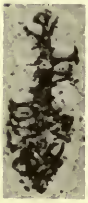
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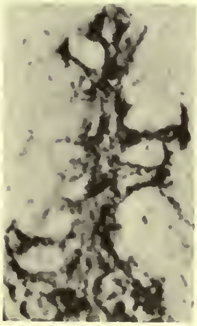
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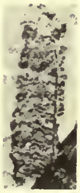
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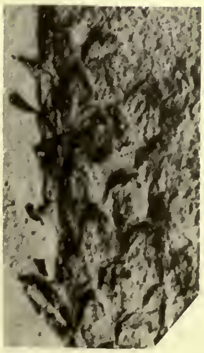
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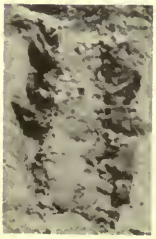
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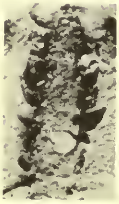
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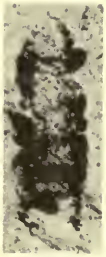
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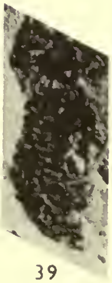
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PLATE 6

Apterocladus lanceolatus gen. et sp. n.

Fig. 40. Holotype, showing attached male cone. LP 6296, ×1.

Fig. 41. Same, ×3.

Figs. 42–44. Branched specimens. Fig. 42, LP 6302, ×1; Fig. 43, LP 6304, ×2; Fig. 44, LP 6303, ×1.

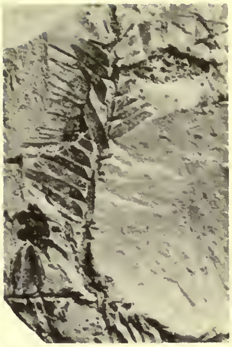
Figs. 45, 46. Male cone showing external surface of microsporophylls. BMNH. no. V.52291, ×3 and ×8.

Figs. 47, 48. Twin male cones. LP 6321, ×1 and ×3.

Podocarpus dubius sp. n.

Fig. 49. A branch. LP 6302, ×1.

Fig. 50. The holotype. LP 6309, ×1.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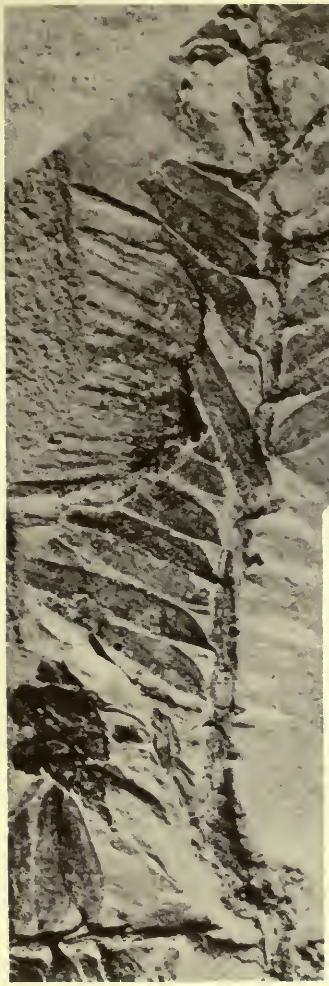
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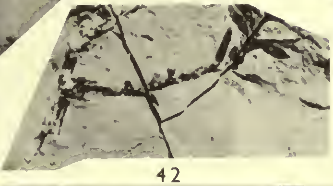
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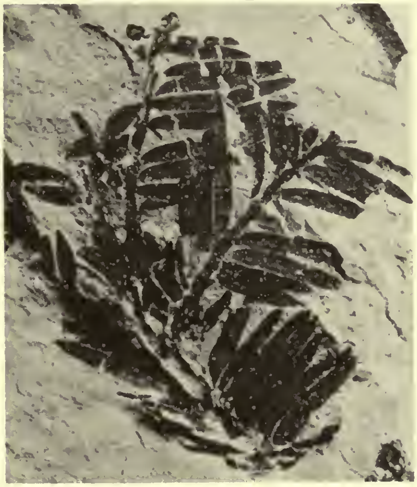
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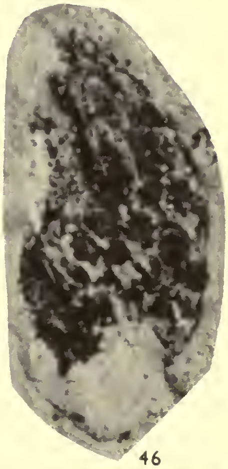
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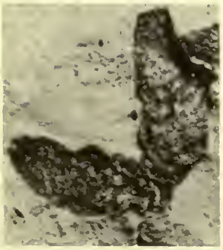
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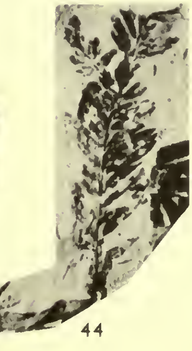
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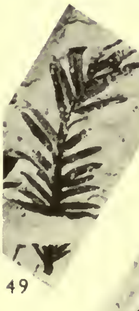
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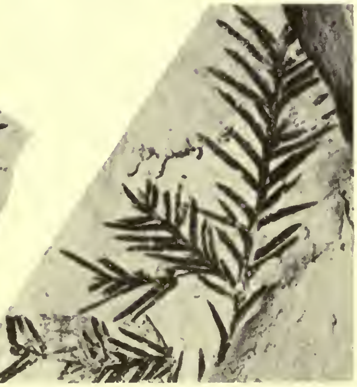
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PLATE 7

Tomaxellia biforme sp. n.

FIG. 51. Stomata of upper cuticle. Slide LP 202, ×500.

Apterocladus lanceolatus gen. et sp. n.

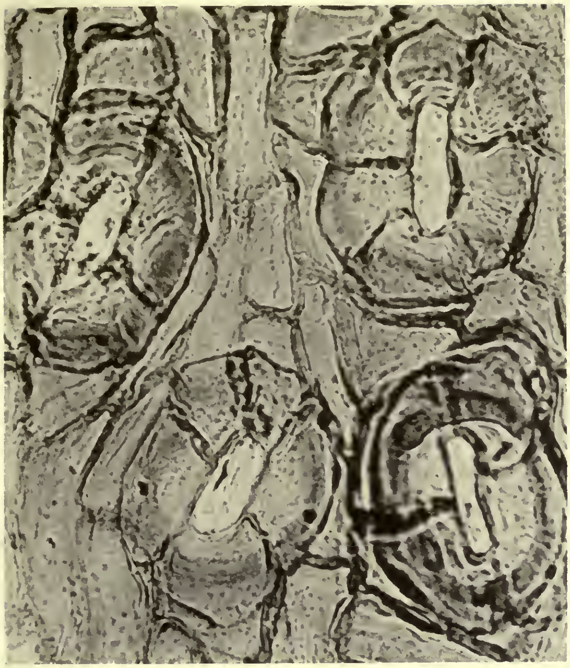
FIG. 52. Stomata in a band. Slide LP 228, ×500.

FIG. 55. General aspect of upper non-stomatiferous (left) and lower stomatifierous (right) cuticles. Slide LP 228, ×100.

Podocarpus dubius sp. n.

FIG. 53. General aspect of both stomatiferous cuticles. Slide LP 225, ×100.

FIG. 54. A stoma. Slide LP 226, ×500.



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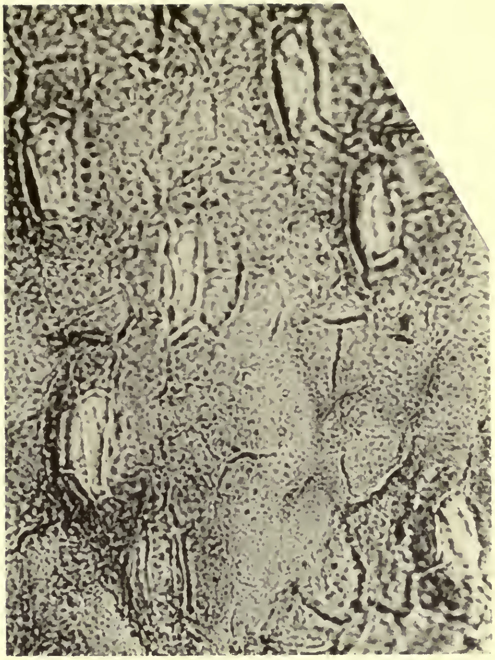

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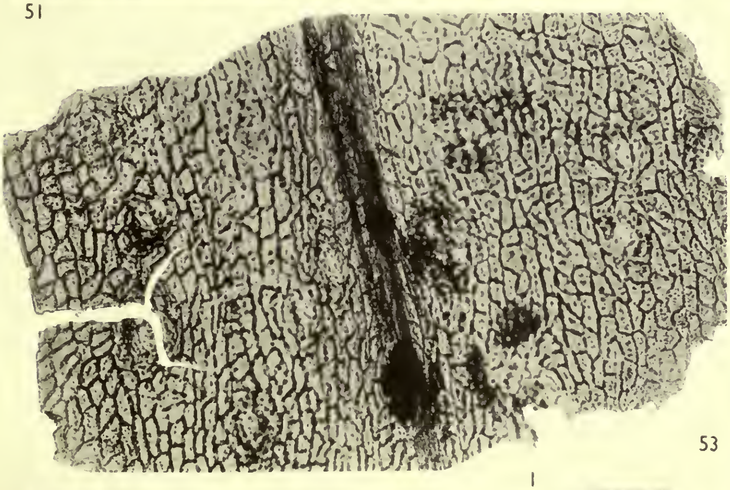

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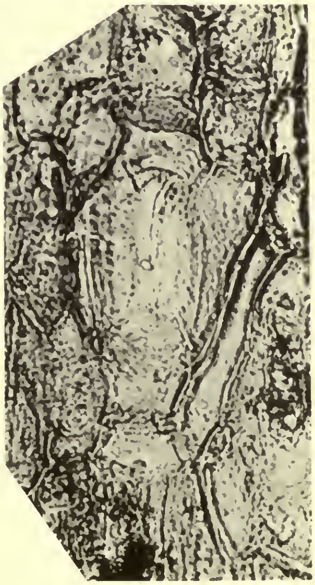

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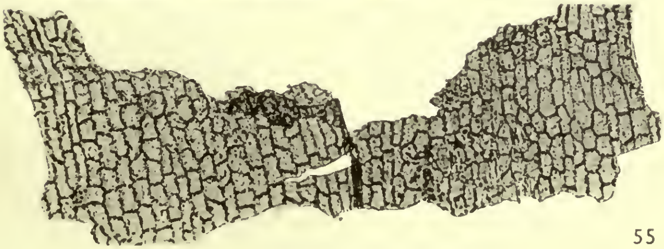

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PLATE 8

Trisacocladus tigrensis gen. et sp. n.

Fig. 56. Slightly macerated seed showing nucellus membrane and remnants of integument. Slide LP 156, ×30.

Fig. 57. Slightly macerated seed showing nucellus membrane and, on top, an oblique mark of enclosed megaspore membrane. Slide LP 157, ×30.

Fig. 58. Integument membrane showing small circular granules adhering to it. Slide LP 166, ×100.

Figs. 59, 60. Pollen. The same specimen in equatorial view at two different focci, showing the exine patterns on the body and contracted air bladders of grain. Slide LP 54, ×1000.

Figs. 61, 62. Pollen. Two specimens in equatorial view showing expanded air bladders. Slide LP 54, ×1000.

Figs. 63–65. Pollen. Polar view of typical grains, showing three small air bladders. Slide LP 54, ×1000.

Fig. 66. Pollen. A grain in polar view. Slide LP 54, ×600.

Fig. 67. Pollen. A grain in equatorial view, showing three bladders. Slide LP 54, ×600.

Apterocladus lanceolatus gen. et sp. n.

Fig. 68. Pollen. Polar view, from cone LP 6296 (Slide LP 229). ×850.

Fig. 69. Pollen. Polar view from another cone, showing incipient 3 sacci. ×700.

Fig. 70. Pollen. Equatorial view showing thickened zone and thin distal exine. ×700.

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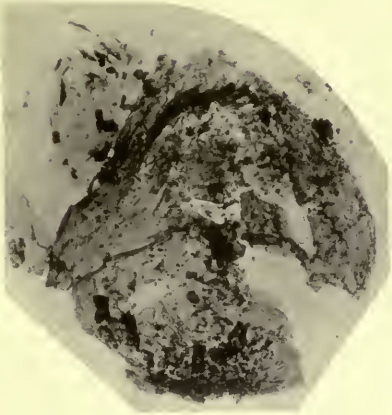
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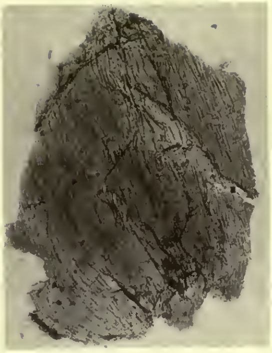
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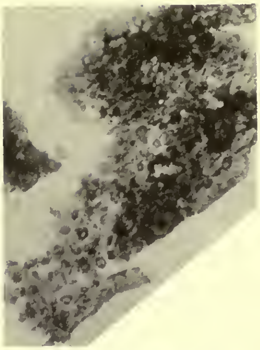
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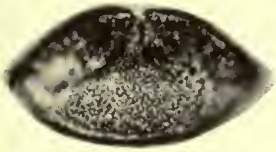
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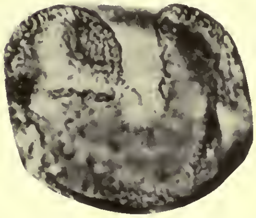
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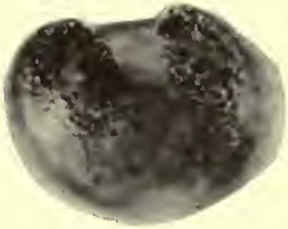
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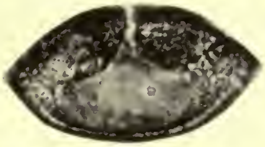
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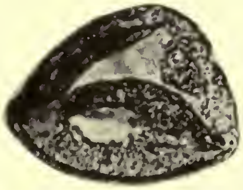
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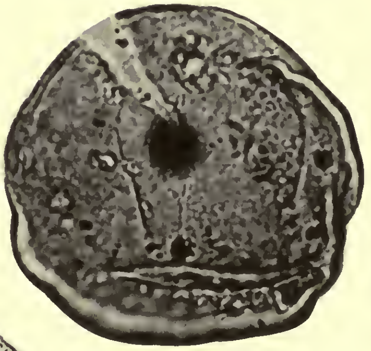
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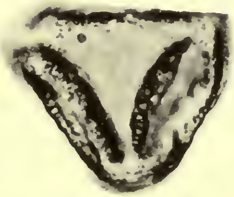
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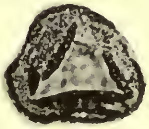
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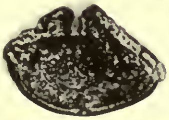
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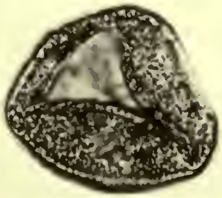
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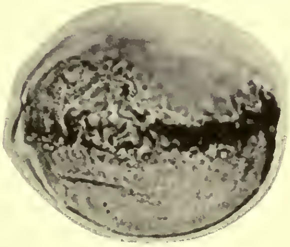
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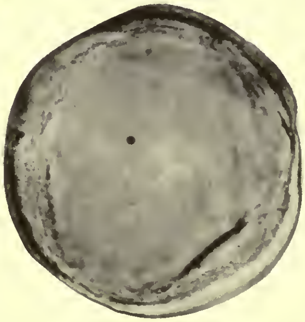
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THE BRITISH SILURIAN CYSTOIDS

C. R. C. PAUL

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 13 No. 6
LONDON: 1967

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THE BRITISH SILURIAN CYSTOIDS

BY

CHRISTOPHER RONALD CHARLES PAUL
Sedgwick Museum, Cambridge

Pp. 297–355 ; 10 *Plates* ; 44 *Text-figures*

BULLETIN OF
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GEOLOGY Vol. 13 No. 6
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In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

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THE BRITISH SILURIAN CYSTOIDS

By C. R. C. PAUL

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SYNOPSIS

The British Silurian cystoid fauna consists of the Echinoencrinitidae and Callocystitidae. It has a very restricted distribution conditioned by depth of water. It ranges from the Wenlock Shale possibly to the Aymestry Limestone. The Echinoencrinitidae originated from the Baltic, the Callocystitidae from N. America.

All the species were permanently fixed except *Schizocystis armata* (Forbes) which was vagrant. The 2- and 3-rhombed forms of *S. armata* had slightly different modes of life. Two trends in feeding, which are widespread among stemmed pelmatozoa, are recognized in the fixed forms. The rhombs were probably respiratory, the two half-rhombs being modified as inlet and outlet. The current pattern derived is widespread among cystoids.

The Glyptocystitida had 7 oral plates not 5, and *Pseudocrinites* has two brachioles representing ambulacra 1 and 4.

The growth of the stem, theca and subvective system is briefly described. Colour bands in the thecal plates may indicate that all species lived less than five years.

The fauna is described. *Tetracystis* and *Prunocystites fletcheri* Forbes are transferred to the Staurocystinae on their ambulacral structure. *Glansicystis* gen. nov. is described for " *Prunocystites* " *baccatus* (Forbes). *Pseudocrinites pyriformis* sp. nov. is described.

I. INTRODUCTION

The British Silurian cystoids form a distinctive and separate element of the British cystoid fauna and it is convenient to deal with them separately. The fauna contains all the British representatives of the families Echinoencrinitidae and Callocystitidae. All but one of the species present have been known since 1848 when Edward Forbes described all the then known British cystoids. This fauna is a particularly important one from the point of view of taxonomy. No less than six of the seven genera present are represented by their type species! It is also important from the point of view of palaeoecology and provides a unique glimpse at the mode of life of these extinct pelmatozoans. Little has been added since 1848 to the descriptions given by Forbes although the number of specimens found has increased considerably. Certain inaccuracies in the original descriptions have survived to the present as a result. The fauna consists of the following :

Family **CALLOCYSTITIDAE** Bernard

Subfamily **STAUROCYSTINAE** Jaekel

Staurocystis quadrifasciatus (Pearce)
Pseudocrinites bifasciatus Pearce
Pseudocrinites pyriformis sp. nov.
Tetracystis oblongus (Forbes)
Prunocystites fletcheri Forbes

Subfamily **APIOCYSTITINAE** Jaekel

Apiocystites pentrematoides Forbes

Family **ECHINOENCRINITIDAE** Bather

Subfamily **SCOLIOCYSTINAE** Jaekel emend.

Glansicystis baccata (Forbes)
Schizocystis armata (Forbes)

II. ACKNOWLEDGMENTS

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Geological Survey & Museum (GSM.), for the loan of material or access to specimens in their care. The author is also indebted to Dr. Mutvei of the Naturhistoriska Riksmuseum, Stockholm (RM.), for the loan of comparative material of *Lovenicystis angelini* and *Echinoencrinites* and to Dr. P. M. Kier of the U.S. National Museum for the loan of specimens of *Pseudocrinites perdewi*. Mr. M. L. K. Curtis of Bristol Museum supplied the information concerning Pearce's types and Dr. I. Strachan and Mr. R. G. Coope of Birmingham University information on the detailed stratigraphy of the Wenlock Limestone at Dudley. Mr. A. Barlow assisted in the preparation of the text-figures.

Very useful discussion on the functioning of the rhombs and the mode of life of *Pseudocrinites* was contributed by Dr. R. P. S. Jefferies and by Mr. P. Minton of Imperial College but the writer alone accepts responsibility for the views expressed in the paper.

This research was completed during the tenure of a Science Research Council research studentship under the direction of Mr. A. G. Brighton, and partly, during the tenure of a Harkness Scholarship, both of which are gratefully acknowledged. Finally the writer wishes to thank Professor O. M. B. Bulman for research facilities in the Sedgwick Museum, Cambridge.

III. GEOGRAPHICAL DISTRIBUTION AND STRATIGRAPHIC RANGE

None of the species dealt with in the present work is known from outside the British Isles and all have a very restricted distribution. Text-fig. 1 shows that this restriction is quite independent of the outcrop distribution and was almost certainly controlled by contemporaneous environmental factors. *Schizocystis armata* (Forbes) occurs in the Wenlock Shale and is found at all the localities shown on Text-fig. 1. The remarkable similarity in distribution shown by *Schizocystis*, in the Lower Wenlock, and the shallow water brachiopod communities established by Ziegler (1965), in the preceding Upper Llandovery, is unlikely to be due to coincidence and it is suggested that the distribution of *Schizocystis* was controlled by depth. All the other species, except *Pseudocrinites pyriformis* sp. nov., are confined to the Wenlock Limestone of Dudley (Wren's Nest and Castle Hill) and possibly the Walsall Inlier also in the cases of *Staurocystis quadrifasciatus*, *Pseudocrinites bifasciatus* and *Glansicystis baccata*. These localities are on the extreme easterly margin of the outcrop of the Wenlock Limestone and may indicate that these species lived in even shallower water. *Pseudocrinites pyriformis* is believed to come from the Sedgley (Aymestry) Limestone of the Sedgley Inlier which is again near the easterly margin of the outcrop and indicates a similar environment for that species too.

Text-fig. 2 shows the succession of cystoid bearing strata at Dudley. *Schizocystis armata* is recorded from Hurst Hill, in the Sedgley Inlier, and Dudley, where only the top 100–150 ft. of the Wenlock Shale outcrop. However, beyond this, little can be said about its distribution within the Wenlock Shale and it may well range throughout the formation. Many museum specimens of the Wenlock Limestone species are preserved on slabs of crystalline limestone composed largely of echinoderm

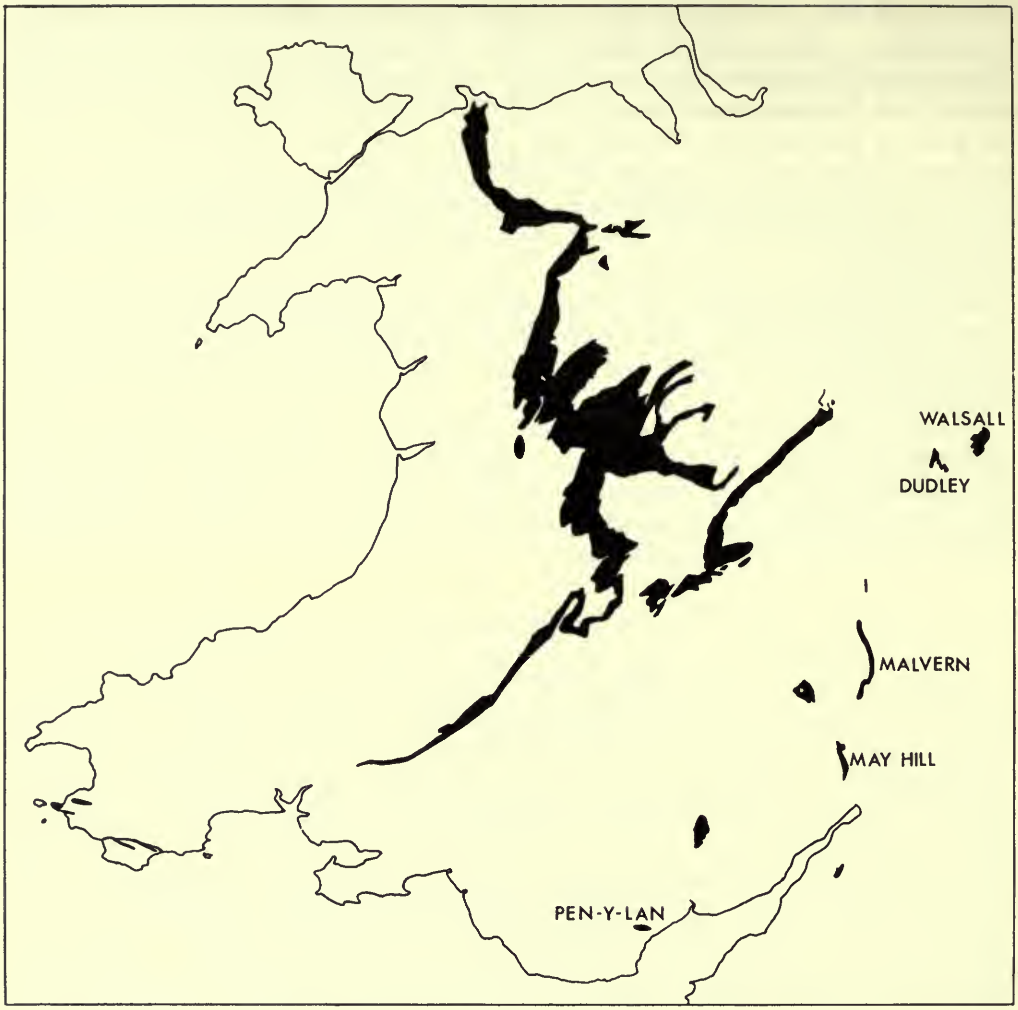


Fig. 1. Map showing the outcrop of rocks of Wenlock and Ludlow age and the cystoid localities. Dudley is used in a broad sense including the Wren's Nest, Castle Hill and the Sedgley Inlier. Compare with the depth zones established in the Llandovery by Ziegler 1965.

debris and with a thin veneer of shale on the surface on which the cystoids are preserved. A large number of crinoids are also found in this type of preservation and both the cystoids and the crinoids are usually well preserved with stems, brachioles and pinnules intact and attached to the thecae or calyces. There is some evidence to suggest that all these specimens originate from the same horizon, namely a shale parting about half way up the Lower Limestone. Almost certainly this horizon represents a catastrophe in which the contemporary echinoderm fauna was exterminated by a sudden influx of mud. There are many other specimens preserved in different lithologies whose exact provenance is unknown however.

The only two specimens of *Pseudocrinites pyriformis* known are in the Holcroft collection in the Department of Geology, Birmingham University. Holcroft was one of the few people who recorded exact localities and these specimens are said to have come from Sedgley. Other specimens in the same collection are recorded as

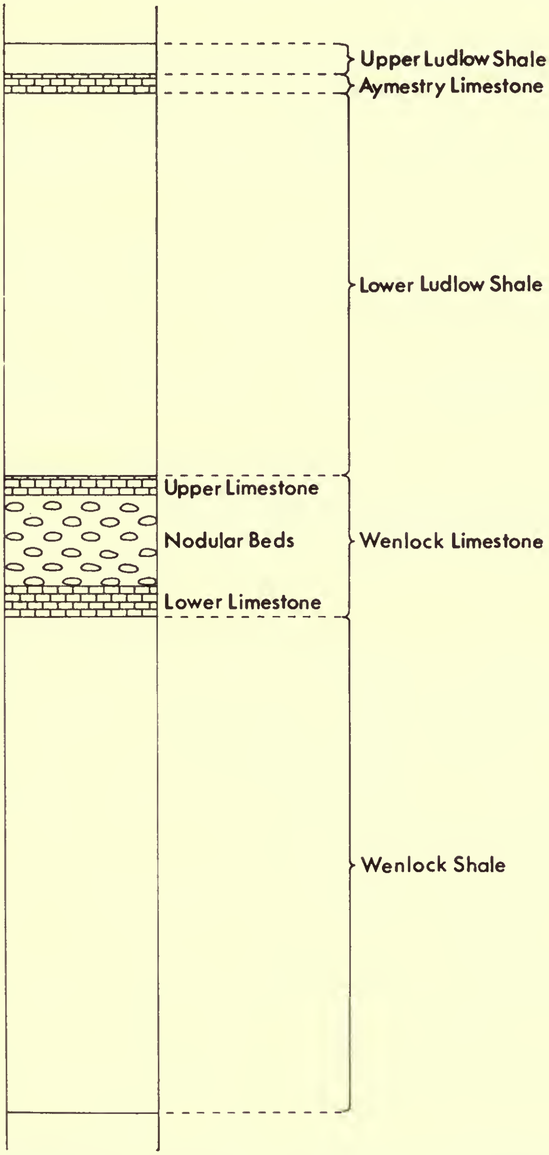

Upper Ludlow Shale
Aymestry Limestone
Lower Ludlow Shale
Upper Limestone
Nodular Beds
Lower Limestone
Wenlock Limestone
Wenlock Shale

FIG. 2. Stratigraphic succession of Silurian cystoid bearing rocks at Dudley.

coming from Hurst Hill, also in the Sedgley Inlier. All the Wenlock rocks in the Sedgley Inlier are confined to the immediate vicinity of Hurst Hill while the vast majority of the Sedgley Inlier, including that part on which Sedgley itself is built, is of Ludlow rocks and both Mr. Coope and Dr. Strachan, of the Geology Department, Birmingham University, inform me that it is likely that these specimens came from the Sedgley Limestone at Sedgley. In this case they are considerably younger than all the other species described here.

IV. RELATIONSHIPS TO OTHER FAUNAS

Schizocystis and *Glansicystis* are endemic to Britain and the last representatives of the Echinoecrinitidae. All other echinoencrinitids are confined to the Ordovician of the Baltic States and Scandinavia. This element of the fauna had a Baltic origin therefore and represents an evolutionary dead end.

Lovenicystis angelini (Jaekel) from Gotland, Sweden, is the only member of the Callocystitidae, apart from the British forms, to occur outside North America. The family ranges from the Upper Ordovician to the Middle Devonian and the British fauna probably represents an evolutionary sideline which migrated across to Europe. It is possible that the Staurocystinae evolved in the British Isles and later migrated back to North America. This subfamily apparently attains its maximum diversity in Britain and appears earlier here than in the United States.

V. FUNCTIONAL MORPHOLOGY AND MODE OF LIFE

In dealing with the morphology of the cystoids it is convenient to consider the stem, the theca, and the subvective system separately.

a. *The Stem*

All the species described had a well developed stem and all except *Schizocystis* probably had a root structure, but it has not been possible to confirm this in *Tetracystis oblongus* or *Prunocystites fletcheri*. The stem is characteristic of the superfamily Glyptocystitida, to which all the present species belong, and is divisible into proximal and distal portions. The proximal portion of the stem is composed of thin, ring-like columnals with a wide lumen, and usually tapers rapidly away from the base of the theca. There are two sorts of proximals : large outer proximals and smaller inner proximals. The outer proximals fit outside the inner proximals and are provided with an internal flange against which the two adjacent inner columnals fit. Externally they may have a flange or a ring of spines or tubercles. Alternating with the outer proximals throughout the proximal portion of the stem are the inner proximals. These are thin rings which are frequently hidden from view by the outer proximals. The internal flange of the outer proximals is provided with two swellings set opposite each other which are interpreted as fulcra. Similarly the upper and lower surfaces of the inner proximals are provided with slight swellings which were probably facets. In *Cheirocrinus* it is known that the fulcra on the upper and lower surfaces of the outer proximals are set at slightly different positions so that the axis of rotation was different for successive pairs of proximals. It has been impossible to confirm that the same arrangement obtained in the British Silurian cystoids but it is certain that the proximal stem was very flexible. Several have been preserved quite tightly curved but still articulated.

The distal portion of the stem was also composed of two sorts of columnals but arranged one above the other. This alternation is not always obvious but was almost certainly present. The distals of both types were relatively tall and narrow in diameter with a narrow lumen. The distal stem generally tapers much less rapidly and in forms with a root structure may not taper at all. The larger distals are the morphological homologues of the outer proximals and are flanged in the species with flanged outer proximals. The smaller distals are, correspondingly, the homologues of the inner proximals. At the termination of the distal stem there is frequently a swelling or some irregular branches which form a root structure. All species with a root structure are believed to have been attached permanently and therefore relied on food-bearing currents coming to them. A flexible stem would be of advantage in that it would allow them to sweep a considerable area around the point of attachment. In forms like *Glansicystis* it would allow the apex of the theca to be directed upwards at all times. It would also allow flexure in currents and thus reduce the chances of the stem snapping. Finally it would raise the theca up off the substrate thus allowing the food collecting apparatus to collect falling food particles before they reached bottom dwelling forms and keep the rhombs and food collecting apparatus well clear of the turbulent zone just above the bottom, reducing the chances of fouling by mud particles. All species without a root structure are believed to have been free and vagrant. Among the present species this includes only *Schizocystis armata* which is believed to have used the stem as an organ of locomotion. *Schizocystis* is a special case and will be dealt with in a separate section.

b. *The Theca*

In *Pseudocrinites* the theca is more or less distinctly lenticular but in all the other species it is ovoid. The mouth was apical and the anus lateral and set fairly high up on the theca. The latter opened in a periproct covered by an anal pyramid surrounded by a single circlet of auxiliary plates. This circlet may be complete or incomplete, apparently even in the same species, and it is difficult to see what function it could have served. It may simply be the remnant of the extensive plated periproctal membrane of the ancestral group, the Cheirocrinidae. The anal pyramid forms a one-way valve system closed either by ligamental or muscular action. There is no indication of any musculature to open the valve and this must be assumed to have been achieved by peristaltic action. As a result the faeces would have been pellet-like and very unlikely to have fouled either respiratory or food bearing currents. Despite its high position on the theca the anus is placed well away from the pectinirhombs which are at the same level as the anus and the single rhomb below it is on the opposite side of the theca. In the Callocystitidae, where the arms are folded down the theca, the food grooves of the brachioles are directed towards the centre of the arms and therefore away from the anus in the ambulacra adjacent to it. There are two orifices higher up on the theca usually accepted as the hydropore and gonopore. One is circular and frequently covered by a pyramid of plates resembling a small anal pyramid. This orifice almost certainly acted as an exit and is therefore accepted as the gonopore. Adoral to it, and curved round it in many cases, is a slit-like orifice provided with a rim and usually swelling out at either end. This is accepted as the hydropore. These two orifices are always above rhomb L1 : R5 and are taken as the fundamental point for orientating the theca. The ambulacrum which passes between the anus and the hydropore and gonopore in the Glyptocystitida is always ambulacrum 5.

The theca of the glyptocystitid cystoids is composed of a definite number of thecal plates arranged in definite circlets. The formula 4 basals (BB), 5 infralaterals (ILL), 5 laterals (LL), 5 radials (RR), and 5 orals (OO) is usually given. The ancestral genus, *Cheirocrinus*, had 6 radials and occasionally examples of other species occur with extra plates but on the whole the formula applies for the first four circlets. In the case of the orals however, it is possible that the usual pentamery of echinoderms has caused the acceptance of too low a number. There were apparently 7 orals in the Glyptocystitida. Kesling (1961*a*, 1961*b*, 1962*a*, 1962*b*) and Kesling & Mintz (1961) have figured the oral areas of *Glyptocystites ehlersi* Kesling, *Jaekelocystis hartleyi* Schuchert, *Rhombifera bohemica* Barrande, *Cheirocrinus anatiformis* (Hall) and *Lepadocystis moorei* (Meek). In all cases there were 7 plates in the oral area and O1 was interpreted as being compound. To these species can be added *Glansicystis baccata* (Forbes), *Schizocystis armata* (Forbes), *Apiocystites pentrematoides* Forbes, *Staurocystis quadrifasciatus* (Pearce) and *Pseudocrinites bifasciatus* Pearce, all with 7 orals. *Pleurocystites* probably had 7 orals too. If all these interpretations are correct 7 orals are known in six of the seven families within the Glyptocystitida and this situation would seem to be of general occurrence. Text-fig. 3 shows the interpretation adopted here. OO2–5 are the same as in all previous interpretations. O1 is the plate bearing the left portions of the gonopore and hydropore as viewed facing these pores. O7 bears the other portions of these orifices and the small plate, adoral to O7, is O6. This interpretation commends itself as in

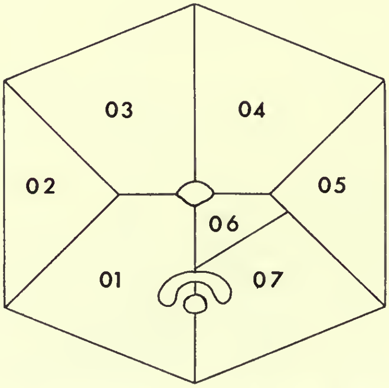


FIG. 3. Schematic representation of the arrangement of oral plates in the Glyptocystitida. OO, orals.

some cases the common suture of O7 and O6 runs from O1 to R5 and in this case the 7 orals form a ring with the plates numbered consecutively.

When fully developed all the rhombs are disjunct pectinirhombs. This type of disjunct pectinirhomb is formed of pore-canals, called dichopores, which are basically folds in the surface of the theca. The walls of adjacent dichopores are confluent and all the dichopores open collectively in *vestibules*. As with all rhombs they are shared between two thecal plates and the common plate suture divides the rhomb into two *half-rhombs*. The width of a rhomb is measured along the plate suture. At right angles to the suture lies the *rhomb axis* which divides the rhomb into two *demi-rhombs* and along which the length of the rhomb is measured. Rhombs in which the length exceeds the width are called *compressed* and the converse *depressed*. When the two half-rhombs are unequal the rhomb is *unequal* and when the two demi-rhombs are unequal it is *asymmetrical*.

Rhombs are developed in three positions in all the species dealt with. These are across the sutures between plates B2 : IL2, L1 : R5 and L4 : R3. As far as is known B2 : IL2 is not developed in *Prunocystites fletcheri* and *Schizocystis armata* sometimes lacks L1 : R5. Otherwise all three rhombs are developed in all species. When fully developed there is a constant difference between the two half-rhombs of each rhomb. The half-rhombs B2, R5, and R3 all have a raised rim on the absutural side of the series of slits and the slits are generally longer than the corresponding slits of the other half-rhombs. In half-rhombs IL2, L1, and L4 there is a continuous raised rim running around the slits on both the ad- and absutural sides. In several cases the slits are very slightly wider in these half-rhombs than in the preceding half-rhombs.

Two trends can be seen in the shape of the rhombs and these can, to a certain extent, be related to the maximum size of the thecae in which they occur. In *Pseudocrinites*, and other genera or species with relatively large thecae, the rhombs tend to be large, depressed and asymmetrical. They are angular in outline and provided with a large number of dichopores. In forms like *Glansicystis*, with relatively small thecae, the rhombs tend to be distinctly compressed, symmetrical and the half-rhombs tend to be semi-circular in outline. The number of dichopores rarely exceeds 10. *Schizocystis*, which has this type of rhomb and a relatively large theca, has an unusually large number of dichopores in its rhombs (up to about 20) but still less than in the rhombs of *Pseudocrinites*.

The constant difference between the two half-rhombs is interpreted as being associated with the functioning of the rhombs. Sinclair (1948) postulated that there were ciliary currents flowing through the dichopores in life. In the rhombs of *Glyptocystites*, which have no absutural rims but an adsutural rim on one half-rhomb, he suggested the rim assisted in preventing re-circulation of the currents. The half-rhomb with the rim was therefore the exit and the other the entrance. All further investigations made by the present writer tend to confirm this interpretation. The closed rim of the rhombs in the present species is interpreted as a mechanical barrier to re-circulation. In *Staurocystis* it is known that the slits of one specimen (BU. Hol, rhomb L1 : R5) are narrower in the incurrent half-rhomb than in the excurrent. This may be a device to prevent harmful particles or organisms entering and clogging the dichopores. The extra length of the incurrent slits may be the result of an attempt to achieve the same cross-sectional area while decreasing the width. Alternatively in some cases the slits of the two half-rhombs appear to be of the same width and in these cases the excurrent would have been stronger than the incurrent. This is known in other cystoids with different types of rhombs and also in blastoids. Thus Macurda (1966) has been able to show that the excurrent from the hydrospires of *Globoblastus norwoodi* was six times as fast as the incurrent. In this case, and in others the present writer has investigated, there can be no doubt as to which way the currents were flowing. Such an arrangement may be of advantage in directing a strong current away from the theca and thus reducing the chances of recirculation by surface ciliary currents.

The trends in the outline of the rhombs are probably a result of the maximum size of the thecae in which they occur. Assuming the rhombs were respiratory, larger thecae would require more oxygen and therefore larger rhombs. This could be achieved by either lengthening the dichopores or increasing their number. The latter is likely to be more efficient since there must be a length in which all the available oxygen will be removed. Increasing the length beyond this will not increase the efficiency of the rhombs. It is significant that in one of the largest rhombs examined by the writer (L1 : R5 in *Pseudocrinites gordoni,* BMNH. E. 23122) the longest dichopore was 6·45 mm. and there were approximately 85 dichopores in 14·85 mm. However, in rhomb L4 : R3 of *Echinoencrinites* cf. *reticulatus* (RM. Ec.5515) the longest dichopore is 6·7 mm. but there are only 9 dichopores in a width of 3·7 mm. Apparently the longest dichopores of both types of rhomb are about the same length. It must be pointed out, however, that the size and shape of a rhomb is controlled by the plates in which it is developed. Thus a rhomb developed across a short suture has a much smaller potential width than one developed across a long one. This in turn is to a certain extent, controlled by the size and shape of the thecae as a whole.

Considering the theca as a whole it is possible to deduce a current pattern for the three rhombs. If the above interpretations are correct then water entered the rhombs at the ab- and adoral extremities of the theca and passed out near the ambitus. In all forms of cystoids in which the current patterns have been determined they are the same, i.e. in at the extremities and out near the ambitus. In *Glyptocystites* and *Cheirocrinus* there were some additional currents running around the theca and *Cystoblastus* and *Rhombifera* represent a departure to a condition where all the currents ran around the theca. Unfortunately sufficiently well preserved specimens of these genera are not available and the current patterns remain unknown in detail.

c. *The Subvective System*

By analogy with living crinoids this system functioned as the food collecting apparatus of the cystoids. The fixed species may be conveniently divided into two groups on the basis of their ambulacral structure. These are: species with the ambulacra folded down the sides of the theca, and those with the ambulacra restricted to the apical region of the test. In the former there are usually four ambulacra but *Pseudocrinites* represents a special case and only has two ambulacra. By analogy with species of callocystitids with the full five ambulacra, the four present in most British species are accepted as 1, 2, 4 and 5, the last being the ambulacrum passing between the anus and the gonopore. For descriptive purposes it is convenient to number the brachioles in each ambulacrum in the order in which they developed.

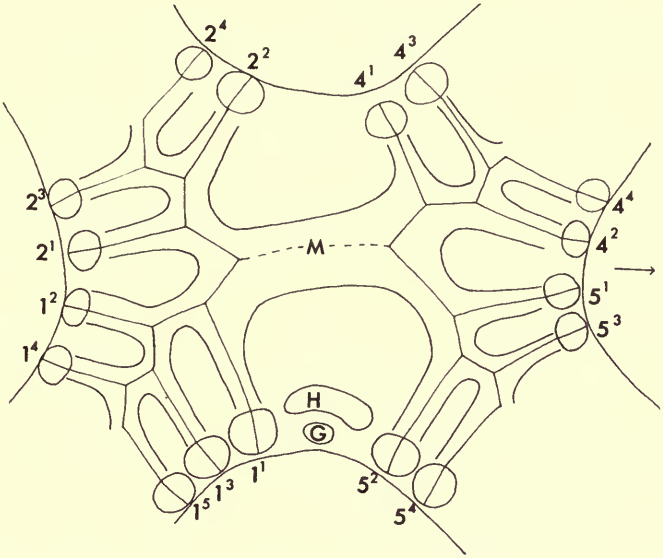


FIG. 4. *Staurocystis quadrifasciatus* (Pearce). Camera lucida drawing of apical region to show arrangement of the ambulacra and brachiole numbering system. G, gonopore; H, hydropore; M, approximate position of mouth. The arrow points to the periproct. The ambulacrum passing between the anus and gonopore is ambulacrum 5. BMNH. 48197.

Thus the first formed brachiole of ambulacrum 2 is 2^1 (see Text-fig. 4). In all the British species the first formed brachiole of each ambulacrum is branched off to the left, looking down the ambulacrum from the mouth to the tip. The second formed brachiole is on the right in all species with four ambulacra and the brachioles alternate regularly throughout the length of the ambulacrum. In both species of *Pseudocrinites* described here there are two facets on the left adapically in each ambulacrum. It is suggested that the two adoral facets are all that remains of the two ambulacra missing in this genus (see Text-figs. 16, 21). Kesling (1961*b*) has shown that the two fully developed ambulacra in *Pseudocrinites* are 2 and 5 and so it is suggested here that the three adoral brachioles in ambulacrum 2 are 1^1, 2^1 and 2^2, while those in ambulacrum 5 are 4^1, 5^1 and 5^2.

The ambulacra in the first group are composed of two series of alternating large and small flooring plates (see Text-fig. 10). The larger alternate about the median line and the smaller are inserted between them at the outside edge. One each of both types contributed to the formation of a brachiole facet with the smaller forming the adoral portion in all cases. Along the zigzag suture between the two rows of primary flooring plates ran the main food groove. At each change of direction it gave off lateral branches running to the brachioles. These were biserial structures with a food groove running down the side facing the main food groove. Both the " arms " and the brachioles were provided with cover plates over their food grooves. It is possible that the cover plates of the " arms " were immobile and therefore that food collection was confined to the brachioles. There were apparently three cover plates to every brachiolar in the brachioles. The structure of the brachioles indicates that they were incapable of twisting about their axes and therefore it would be advantageous to have the food grooves facing any food bearing currents. From the disposition of the ambulacra food collecting would seem to have been confined to four, or in *Pseudocrinites* two, *zones of collection.* The brachioles were capable of curling inwards over the ambulacrum. It is not certain whether this was a protective action or simply the position adopted when at rest. When feeding the brachioles would have been extended and this was probably achieved by hydrostatic action. If so the orientation of the facets gives an indication of the width and cross-section of the zones of collection.

Pseudocrinites would seem to have been at a disadvantage compared with the other species. Not only did it have half the potential number of brachioles of its nearest relative, *Staurocystis quadrifasciatus*, but the brachioles were set further apart. There were also only two dozen brachiolars in each brachiole in *P. bifasciatus* as opposed to three dozen in *Staurocystis.* From the lenticular shape of the theca of *P. bifasciatus* one may infer that if it turned edge-on to any currents it would have brought one zone of collection to face the current and reduced resistance to the current. If the current periodically reversed both zones could function with very little twisting of the stem. The most obvious reversing current is a tidal one. *Pseudocrinites pyriformis* presumably had a similar mode of life although it had longer brachioles and ambulacra which did not extend as far down the sides of the theca.

In *Glansicystis*, and possibly also *Prunocystites*, the brachioles are grouped about the mouth and the food grooves on the theca are very short. The brachioles have their food grooves on the adoral side and thus form an apical *cone of collection.* This arrangement is much better adapted to collecting falling food particles. From the position of the food collecting apparatus it may be inferred that the British Callocystitidae were better adapted to take advantage of currents in a relatively agitated sea while *Glansicystis* was better able to take advantage of falling food particles in a relatively still sea. These appear to be two extreme conditions which are found randomly distributed among stemmed Pelmatozoa.

d. *Schizocystis armata* (Forbes)

As mentioned previously this species differs in most respects from all the others dealt with. It is found over a much wider, though still restricted, area. It is apparently confined to the Wenlock Shale and thus lived in a muddy environment. In its morphology it has one very important difference in lacking a root structure.

Kirk (1911) has shown that many stemmed pelmatozoa were in fact vagrant. It is unfortunate that he chose as some of his examples British Silurian species which are now known to have been attached permanently but his main contention is not invalidated by this. It is not unreasonable to assume that all stemmed pelmatozoans which lack a definite root structure were voluntarily vagrant, at least temporarily, during their life-time. If food supplies were erratic temporary fixation would only be of advantage if the animal could voluntarily free itself. One must infer that forms like *Ancyrocrinus* literally weighed anchor and sought new feeding grounds in times of short supply. Such activity is known in Recent free living crinoids (which in general lack a stem) and may be inferred for extinct ones. On the above reasoning *Schizocystis* was probably vagrant, and used its stem as a tail.

The theca, like the stem, is on the same basic plan as the other species but has differences in detail. It is very variable in form and ornamentation but is generally compressed adorally and this may be an attempt to develop a bilateral symmetry. Taking the anus as posterior the compression is lateral and the two flattened areas correspond to the left and right sides. In many examples the right side is gently convex throughout but the left side is concave or flat adorally and convex aborally. The rhomb L1 : R5, which is often undeveloped, lies on the left side of the theca.

There are two ambulacra, running posteriorly and anteriorly along the crest of the theca. The posterior ambulacrum is the shorter and sometimes reaches the periproct. A curious feature of the ambulacra is that brachioles are developed predominantly on one side only. Brachioles are mainly developed on the left sides of both ambulacra and as a result the food grooves face the left side of the theca in the posterior ambulacrum and the right side in the anterior ambulacrum.

It is reasonable to assume that this species was benthonic, and since it lacks a root structure, that the theca lay on the substrate. Placing a theca on a flat surface the most stable position for it is lying on the left side. In the two-rhombed forms this leaves both rhombs clear of the substrate and the mud is unlikely to have fouled the rhombs. This is also true of the gonopore and hydropore which are developed on the left side in a raised portion of the test which is vertical in this orientation. The brachioles of the posterior ambulacrum could browse off the mud while those of the anterior ambulacrum would have their food grooves facing upwards and could possibly have fed off falling food particles. When the third rhomb is present it would have been useless in this orientation as it would have been fouled by the mud as would the gonopore and hydropore. The weight of the stem may have been used as a counterbalance to the theca and so the adoral part may have been kept off the substrate. There are difficulties in this suggestion. If the substrate was muddy the theca would have sunk in to some extent and the zone immediately above the surface would have been muddy if there was even slight turbulence. Possibly three-rhombed forms could tolerate having one inefficient rhomb since the two-rhombed forms tolerated the complete loss of one. It is difficult to explain the orientation of the food collecting apparatus and either this species was relatively poorly adapted to its new mode of life or it was trying to get the best of both worlds, feeding in the usual manner for the Echinoencrinitidae and browsing off the mud as well.

VI. GROWTH

a. *The Stem*

Plotting the graph (Text-fig. 5) of thecal height against the number of proximal columnals in *Staurocystis quadrifasciatus* indicates that there is considerable variation. A slightly better grouping is obtained by plotting the diameter of the top-most columnal against the total number of proximals (Text-fig. 6). Growth of the proximal stem was almost entirely confined to the addition of new columnals and this most likely took place at the base of the theca, as in living crinoids. In the distal stem growth was partly achieved by the addition of new distals and partly by the lengthening of existing distals. Since the large and small distals alternate regularly, in many cases, addition of new distals could not have been by the intercalation of " internodals " as in some crinoids. It is very unlikely that proximals migrated relatively down the stem and turned into distals after reaching a given point. This would require considerable changes in shape and the inner proximals would have to emerge from within the outer proximals. Almost certainly new distals were added at the junction of the distal and proximal portions of the stem and in some cases the topmost distals are thinner than succeeding ones and appear to be relatively newly formed.

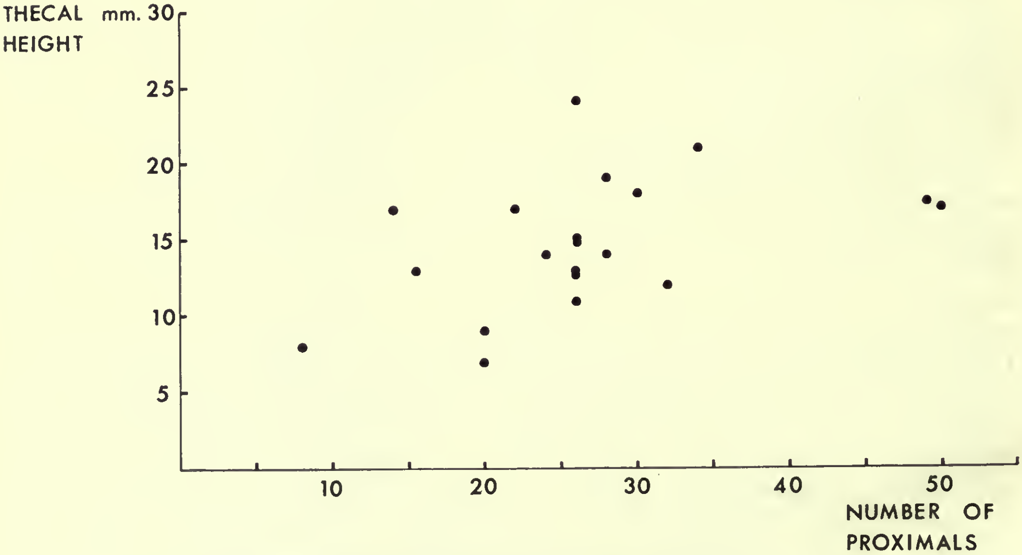


FIG. 5. *Staurocystis quadrifasciatus* (Pearce). Graphical representation of relationship between thecal height and number of proximal columnals.

b. *The Theca*

All thecae known have the same number of thecal plates and within the size range examined growth was achieved by increasing the size of these plates and not by the addition of new plates. The smallest thecae known are still quite large, about 5 mm. in thecal diameter, so the earliest growth stages remain unknown. Fine growth lines are not very often preserved in these cystoids but growth can be shown to have been holoperipheral in all thecal plates. Some specimens of all species show colour banding on the plates which is associated with growth. This is most clearly shown in SM. A11160, a worn specimen of *Tetracystis oblonga* showing, on all plates visible, concentric light and dark bands. These bands are thickest where growth has been greatest and thinnest where growth has been least. B3 shows a central light coloured area followed outwards by four alternating dark and light bands and the suggestion of another dark band at the suture. These bands can be matched in other plates but in general the central light area is smaller relatively, particularly on the only radial plate clearly visible (R5). Measuring outwards from the centre of B3 towards the common suture with IL3, the thicknesses of the bands are as follows: 0·6 mm. 0·23 mm. 0·53 mm. 0·33 mm. and 0·27 mm., the vague suggestions of the outermost dark band are too indefinite to measure. The darker bands are generally thinner as is the case above (see Pl. 10, figs. 6, 13). Apparently the growth was periodic and the periods when darker calcite was deposited were either shorter or less favourable to calcite secretion. This was almost certainly a seasonal effect in which case the animal commenced growing in season favourable to calcite secretion and survived two lean periods, possibly up to the onset of a third. If these periods were annual, which is the most obvious suggestion, then the dark bands probably represent winter and this cystoid reached its present size in three years. No example seen exceeds five years. There is apparently no information on longevity and growth rates in living crinoids but in echinoids corollary growth rates can be found. The information available in four species gives coronal diameters of 24–90 mm. in three years (Hyman 1955: 588), whereas the cystoid is 14 by *c.* 8 by *c.* 11 mm. The mode of growth of

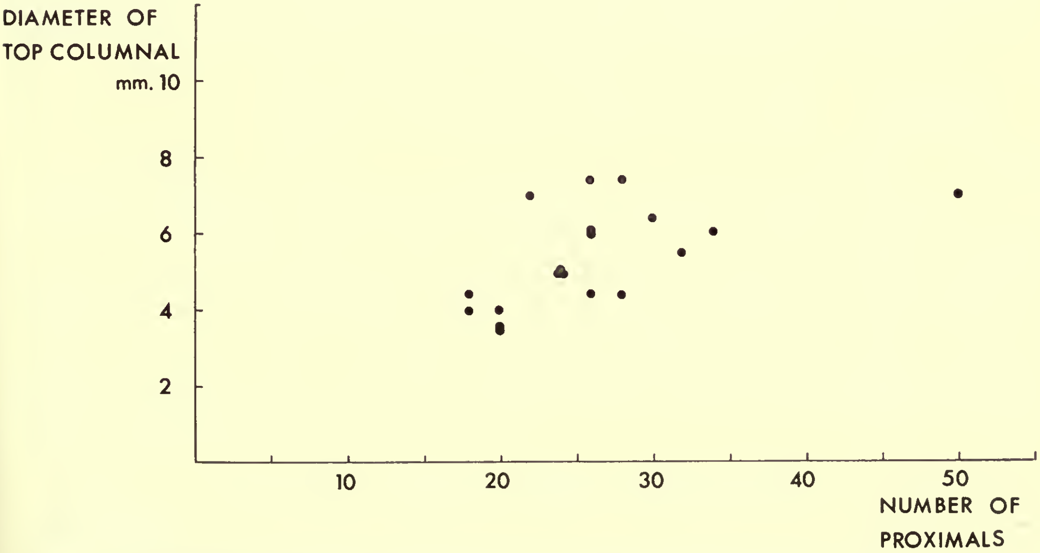


Fig. 6. *Staurocystis quadrifasciatus* (Pearce). Graphical representation of relationship between diameter of topmost proximal columnal and number of proximal columnals.

echinoids is quite different at least initially, and so not much importance can be attached to this information.

The primary orifices of the thecae of the species described here all open across plate sutures and this is interpreted as being for mechanical convenience in growth. Enlargement of these orifices was achieved by a lack of secretion of calcite in the plates surrounding them and not by resorbtion. The slits of the pectinirhombs also grew initially by primary non-secretion of calcite. Once the slits become disjunct they could only increase in size by resorbtion. In *Lovenicystis angelini* the evidence suggests that no resorbtion occurred but apparently it did occur in *Schizocystis armata*. All the rhombs commenced as a single slit and grew by the addition of slits laterally. As the plates bearing the two half-rhombs became larger the slits became longer and beyond a certain length they became disjunct. In a fully developed rhomb all the slits are disjunct and the rims are well developed. In the present type of rhombs the spacing of slits is very constant as is their width. Internally both the dichopores and inter-dichopore spaces are approximately 0·10 mm. wide and in the majority of cases there is one dichopore and one inter-dichopore space in a width of 0·19–0·21 mm. Almost certainly this constancy of width is due to the combined thicknesses of cilated epithelium, and lengths of cilia, lining the dichopores. The fact that the inter-dichopore spaces in this type of rhomb are also of the same width indicates that these too were lined with ciliated epithelium.

c. *The Subvective System*

The ambulacra grew by the addition of flooring plates distally. In the Callocystitidae the ambulacra are wider, and the individual flooring plates thicker and wider, adorally. This suggests the last formed flooring plates were distal. There is no evidence for the addition of flooring plates adorally and it would be difficult to

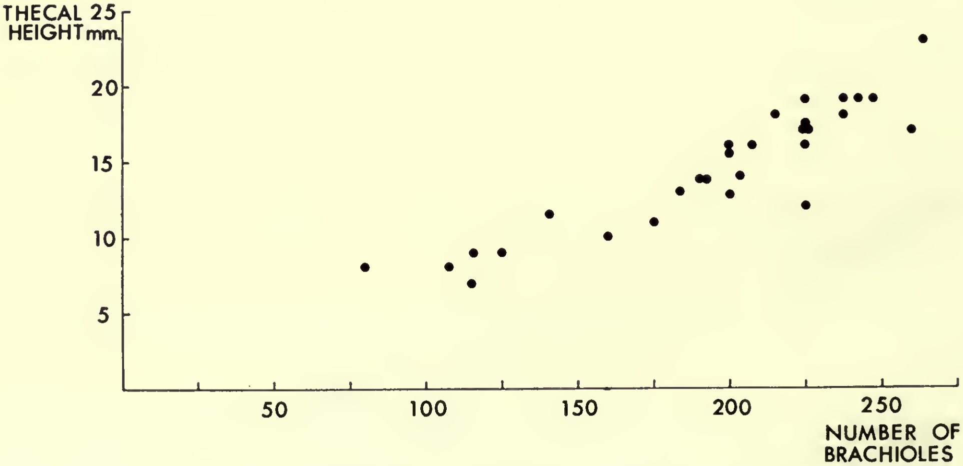


Fig. 7. *Staurocystis quadrifasciatus* (Pearce). Graphical representation of relationship between thecal height and total number of brachioles.

maintain the arrangement of brachioles in which the most adoral brachiole in each ambulacrum was branched off to the left.

Each pair of flooring plates added gave rise to another brachiole and these apparently grew rapidly as in no case have distal brachioles been found significantly shorter than the adoral ones. The brachioles grew by the addition of brachiolars distally. Kesling (1961*b*) found that the spacing of brachioles in *Pseudocrinites gordoni* Schuchert remained almost constant throughout growth and was a useful specific character. This can be confirmed for *Pseudocrinites bifasciatus* and *Staurocystis quadrifasciatus* (see Text-fig. 7) but the spacing of brachioles in *Tetracystis oblongus* and *Apiocystites pentrematoides* varies considerably. This variation is not necessarily related to growth. In species with an almost constant spacing of brachioles it is found that the spacing is slightly wider adorally, presumably due to the increased thickness of the ambulacral flooring plates.

In species with a constant spacing of brachioles, and probably in the others as well, there was considerable readjustment of the flooring plates with respect to the thecal plates throughout growth. As growth proceeded any one flooring plate migrated adorally relative to the thecal plates. Thus, for example, in *Pseudocrinities bifasciatus*, BU. H012 has a thecal height of 7 mm. and an estimated 12 brachioles in ambulacrum 2. Brachiole 2^{12} lay on IL2 just above the common suture with B3. In SM. A12593 (thecal height 16 mm.) brachiole 2^{12} lay on R2 just above the common suture with L3. Thus if these brachioles are homologous, as is suggested here, brachiole 2^{12} migrated across an infralateral and a lateral onto a radial plate between the two growth stages represented by these two specimens.

VII. SYSTEMATIC DESCRIPTIONS

Superfamily **GLYPTOCYSTITIDA** Bather 1899

Family **CALLOCYSTITIDAE** Bernard 1895

Subfamily **STAUROCYSTINAE** Jaekel 1899

DIAGNOSIS. A subfamily of Callocystitidae with 2–4 strongly protruding ambulacra developed on smooth bands on theca and not in shallow grooves.

In the classification which will be adopted in the forthcoming Treatise on invertebrate palaeontology (Kesling 1963) only two genera are referred to this subfamily, *Staurocystis* and *Pseudocrinites*. *Tetracystis*, which has hitherto been assigned to the Apiocystitinae, has very similar protruding ambulacra developed on smooth bands on the theca, and is here included in this subfamily on these grounds. *Prunocystites fletcheri*, the type species of *Prunocystites*, also has protruding ambulacra and so this species is included here as well.

Genus ***STAUROCYSTIS*** Haeckel 1896

Lepadocrinus of authors.

TYPE SPECIES. *Pseudocrinites quadrifasciatus* Pearce 1843.

Diagnosis. A genus of Staurocystinae with ovate theca and four ambulacra all reaching the stem, brachioles closely spaced, relatively long lateral food grooves and ambulacral cover plates frequently preserved.

At present there is only one species. Haeckel (1896*a* : 166) introduced the name *S. cruciata* but this is a nomen nudum. *S. oblongus* (Forbes) Haeckel = *Tetracystis oblongus* (Forbes), see p. 330.

Staurocystis quadrifasciatus (Pearce)

(Pl. 1, figs. 1–8; Pl. 2, figs. 1–3; Pl. 10, figs. 1–5, 12; Text-figs. 4–13)

1843*a*	*Pseudocrinites quadrifasciatus* Pearce : 160.
1843*b*	*Pseudocrinites quadrifasciatus* Pearce : 472.
1843*c*	*Pseudocrinites quadrifasciatus* Pearce : 265.
1844	*Pseudocrinites quadricopuladigiti* Garner : 160, pl. a, fig. 14.
1848	*Pseudocrinites quadrifasciatus* Pearce ; Forbes : 498 ; pl. 13, figs. 1–13.
1854	*Pseudocrinites quadrifasciatus* Pearce ; Murchison : 216, text-fig. 37, fig. 2.
1857	*Pseudocrinus quadrifasciatus* (Pearce) Pictet : 298, pl. 99, fig. 13.
1867	*Pseudocrinites quadrifasciatus* Pearce ; Murchison : 222, 513, text-fig. 55, fig. 2.
1868	*Pseudocrinites quadrifasciatus* Pearce ; Bigsby : 26.
1873	*Pseudocrinites quadrifasciatus* Pearce ; Salter : 127.
1875	*Pseudocrinites quadrifasciatus* Pearce ; Bailey : 54, pl. 18, figs. 6*a–c*.
1876	*Pseudocrinites quadrifasciatus* Pearce ; Quenstedt : 680, pl. 113, figs. 77, 78*a–d*.
1891	*Lepadocrinus quadrifasciatus* (Pearce) Woods : 43.
1891	*Pseudocrinus quadrifasciatus* (Pearce) ; Carpenter : 7, 10.
1896*a*	*Staurocystis quadrifasciatus* (Pearce) Haeckel : 134, pl. 3, figs. 1–3.
1897	*Lepadocrinus quadrifasciatus* (Pearce) ; Bather : 101, fig. 156.
1899	*Staurocystis quadrifasciatus* (Pearce) ; Jaekel : 286, text-fig. 61, pl. 14, figs. 1, 2.
1900	*Lepadocrinus quadrifasciatus* (Pearce) ; Bather : 62, text-fig. 30.
1904	*Staurocystis quadrifasciatus* (Pearce) ; Schuchert : 227.
1938	*Lepadocrinus* Spencer, pl. 2, fig. b.
1943	*Staurocystis quadrifasciatus* (Pearce) ; Bassler & Moodey : 53, 191.
1964	*Lepocrinites quadrifasciatus* (Pearce) Castell : 100, pl. 24, fig. 1.

Diagnosis. As for the genus.

Holotype. Pearce's original specimen (Bristol Museum Ca.7860) was destroyed in an air-raid on 24th November, 1940. As the species is readily recognized and there is no point of taxonomy to be settled there is no need to designate a neotype.

Material. About 140 specimens in BMNH., BU., DL., GSM., OUM., RSM., SM.

Horizon and locality. Wenlock Limestone, Middle Silurian ; Dudley (Tividale, Wren's Nest, Castle Hill) and Walsall.

Description. The theca is subovate to subquadrate and provided with four ambulacra running down the sides from the apex to the insertion of the stem. The mouth, hydropore and gonopore are apical and the anus lateral. The theca was attached to the substrate by a stem provided with a root structure.

The thecal plates are arranged according to the usual formula. The arrangement of the plates of the first four circlets is as in Text-fig. 8 and of the orals as in Text-fig. 9. The position of the ambulacra may vary slightly and four plates may surround the

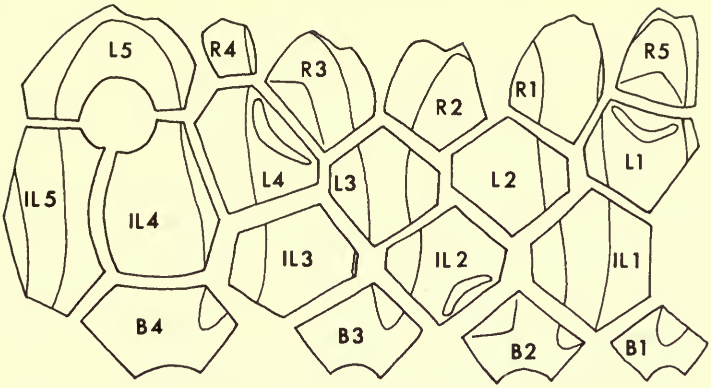


FIG. 8. *Staurocystis quadrifasciatus* (Pearce). Sketch of arrangement of thecal plates of the first four circlets. BB, basals ; ILL, infra-laterals ; LL, laterals ; RR, radials. Based on specimen SM. A.28230.

periproct in some cases. Otherwise there is little variation in the plating arrangement. The four basal plates unite abapically to form a circular cicatrix 4·4 mm. in diameter in SM. A28230. All the plates are ornamented with radiating and concentric ridges which are often discontinuous and give the surface a malleated appearance. This ornament is only developed on the portions of the plates which do not under-lie the ambulacra. These latter portions are smooth bands on which traces of the outlines of the ambulacral flooring plates show in well preserved examples.

Three disjunct pectinirhombs are developed in all examples and are placed in the three inter-ambulacral areas which do not contain the periproct. B2 : IL2 lies in

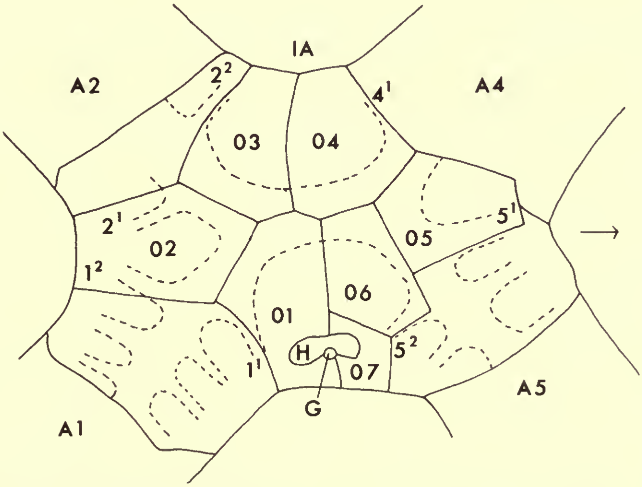


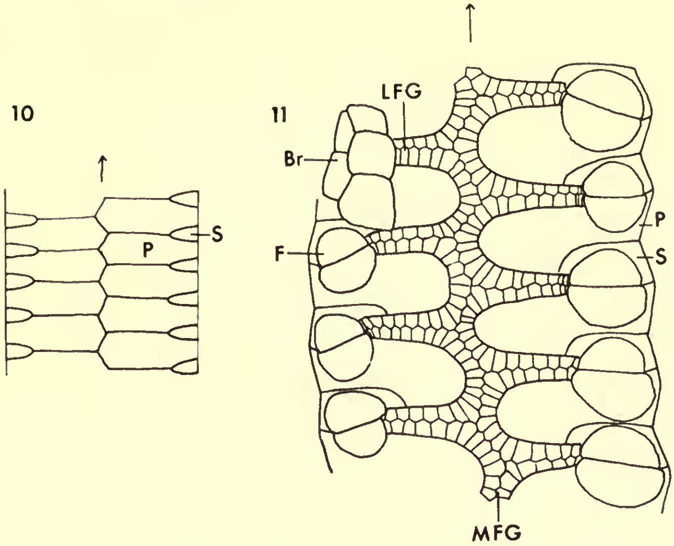
FIG. 9 *Staurocystis quadrifasciatus* (Pearce). Camera lucida drawing of apical region of slightly weathered specimen, showing arrangement of orals and positions of ambulacra. AA, ambulacra ; G, gonopore ; H, hydropore ; IA, inter-ambulacrum ; OO, orals. The arrow points to the periproct. BU. Ho1.

the anterior inter-ambulacrum, L1 : R5 in the left and L4 : R3 in the right. In young specimens all or some of the pectinirhombs may be completely or partially conjunct. B2 : IL2. (BU. H069) this rhomb is depressed in outline, angular and measures 5·0 mm. by 3·7 mm. externally. B2 has an open rim while IL2 has a closed rim. There are 25 dichopores in a width of 4·35 mm. and the longest reaches 3·2 mm. The slits are 0·07 wide and reach a length of 0·9 mm. on B2 but only half that length on IL2. BMNH. E.16353–54 are two sections through this rhomb from a single specimen. Both sections are transverse and approximately parallel to the suture. In E.16353 (Pl. 10, figs. 2, 3) all the dichopores open at the surface apparently. There are 19 dichopores in a width of 3·9 mm. The outline of the section is a symmetrical triangle with the deepest dichopore at the centre. This dichopore is at least 1·2 mm. deep. The dichopores and inter-dichopore spaces are both very evenly spaced and average about 0·1 mm. in width. The dichopore walls are very thin and average about 0·015 mm. By comparison with a complete theca it is possible to infer that the section was through the half-rhomb B2. This is the only section which could pass along an ambulacrum as this one does.

E.16354 is in the same rhomb but cut nearer the suture apparently, as the deepest dichopore is deeper than in E.16353. There are only 18 dichopores in a width of 3·75 mm. They decrease in depth towards the left of the section in much the same way as in E.16353 but at a slower rate towards the right. The deepest dichopore is 1·75 mm. but the right marginal dichopore is still 1·6 mm. deep. The width of the dichopores and inter-dichopore spaces is the same however. There is an odd appearance of a membrane surrounding the entire set of dichopores internally which, under crossed nicols, coincides with a slight change in optical orientation of two calcite crystals. This could conceivably be due to the section being slightly oblique to the plate suture between B2 and IL2 and therefore passing through calcite in optical continuity with both plates. Similar "membranes" described as surrounding the hydrospires of some blastoids also coincide with optical discontinuities between calcite crystals filling the thecae (Joysey, personal communication, July, 1966).

L1 : R5. (BU. H01). This rhomb is depressed, angular and measures 3·0 mm. by 5·33 mm. externally. There are 24 or 25 dichoposes in a width of 4·8 mm. and the longest dichopore is 2·53 mm. long. The slits on R5 are regularly 0·07 mm. wide and the inter-dichopore spaces 0·125 mm. The longest slit in R5 reaches 1·07 mm. and that in L1 0·67 mm. Although the adsutural portion of the rhomb rim is not completely developed the thecal wall is more strongly raised adjacent to the slits on L1 than on R5. The slits in L1 are 0·09 mm. wide and separated by 0·107 mm.

L4 : R3. (BU. H042). It is slightly immature depressed, asymmetrical and with an angular outline. It measures 5·13 mm. by 2·93 mm. externally and has 27 dichopores in a width of 5·0 mm., the longest reaching 2·37 mm. There are 9 dichopores in the demi-rhomb adjacent to ambulacrum 4, and 18 in the demi-rhomb adjacent to ambulacrum 2. The slits in half-rhomb R3 are 0·07 mm. wide and reach a maximum length of 0·9 mm. adaxially. Those in L4 vary from 0·09–0·107 mm. in width and reach approximately 0·6 mm. in length. The slits in R3 are separated by 0·125 mm. and those in L4 by 0·09–0·107 mm. In this rhomb one or two marginal dicho-



Figs. 10, 11. *Staurocystis quadrifasciatus* (Pearce). Fig. 10. Sketch of impression of ambulacral flooring plates on the thecal plates, near top of an ambulacrum. P, primary flooring plate ; S, secondary flooring plate. Based on specimen SM. A.28230. Fig. 11. Camera lucida drawing of part of an ambulacrum. Br, brachiole ; F, facet ; LFG, lateral food groove ; MFG, main food groove ; P and S as in Fig. 10. The arrows point to the mouth. Based on specimen SM. A.11156.

pores are conjunct and the adsutural rim is virtually undeveloped. However BMNH. 47908 shows a fully developed rhomb which is even more asymmetrical and has a complete closed rim on L4 and only an absutural rim on R3. BMNH. 57385 is particularly interesting as the demi-rhomb adjacent to ambulacrum 4 is only partly formed and apparently its growth was inhibited by the presence of the ambulacrum (see Pl. 2, fig. 2).

The mouth has not been directly observed but presumably lay apically at the confluence of the four ambulacra (see Text-fig. 4). It was surrounded by 7 orals arranged as in Text-fig. 9. The ambulacra were developed on broad bands on the theca. These bands are 4·0 mm. wide at the apex in SM. A28230 and taper very gradually towards the tips. The primary ambulacral flooring plates were very thin and narrow and the secondary flooring plates were very small in comparison and did not reach the ambulacral mid-line (see Text-fig. 10). The brachiole facets are small kidney-shaped areas and are in contact with each other. Their spacing appears to have been almost constant throughout growth. The average of ten measurements, taken from five specimens (one near the tip and one near the mouth for each) was 5 brachioles in 3·59 mm. The variation was from 5 in 3·2 mm. to 5 in 3·8 mm. The constancy of this feature during growth is also indicated to a certain extent by Text-fig. 7. The main and lateral food grooves of the ambulacrum are provided with cover plates which apparently did not articulate with the flooring plates in life and formed a permanent roof over the food groove. They are very narrow plates, about

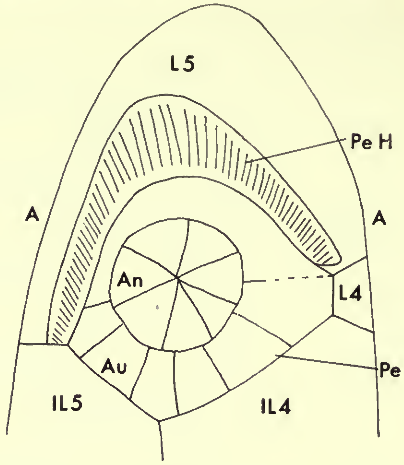


Fig. 12. *Staurocystis quadrifasciatus* (Pearce). Camera lucida drawing of area around periproct, showing four plates surrounding the periproct. AA, ambulacra ; An, anal pyramid ; Au, auxiliary circlet ; ILL, infralaterals ; LL, laterals ; Pe, periproct (comprising anal pyramid and auxiliary circlet) ; Pe.H, periproct hood. Cf. Pl. 1, fig. 7 ; Pl. 2, fig. 3. BMNH. 48197.

half the width shown in Text-fig. 11, and are apparently unornamented. Between the lateral food grooves the primary flooring plates are ornamented with a large central tubercle and occasionally another smaller tubercle close to the main food groove (see Pl. 2, fig. 3). The brachioles are composed of about 3 dozen regularly alternating brachiolars and are about 6–8 mm. long. They have a central straight food groove, about 0·2 mm. wide and provided with cover plates. There are three cover plates per brachiolar. In BMNH. E.7512 the brachioles are 0·7 mm. wide at the base and taper gradually throughout their length to 0·4 mm. near the tips.

The periproct is surrounded by three thecal plates in most cases. These are, in increasing order of contribution to the border : IL5, IL4, L5. Occasionally L4 also reaches the periproct and contributes to a very small portion of the border. L5 frequently surrounds half the periproct and is provided with a special structure immediately adoral to the periproct here termed the *periproct hood* (Text-fig. 12). The periproct may be circular or bell-shaped and contains an anal pyramid reaching 3 mm. in diameter and composed of 5–7 anals. The anal pyramid is surrounded by a circlet of auxiliaries which may be open or closed and consists of about 9 plates. Both the anals and auxiliaries may have slightly raised margins.

The gonopore and hydropore are apical and shared by O1 and O7, as is usual. The gonopore is a small circular opening 0·25 mm. in diameter in BU. Ho1. Adoral to it and slightly curved around it is the hydropore which is provided with a rim. BMNH. 57381, which has the oral area ground down, shows an embayment in the internal margin of the thecal wall just below the point of emergence of these orifices (see Text-fig. 13).

The stem is very variable in length and relative proportions of the proximal and

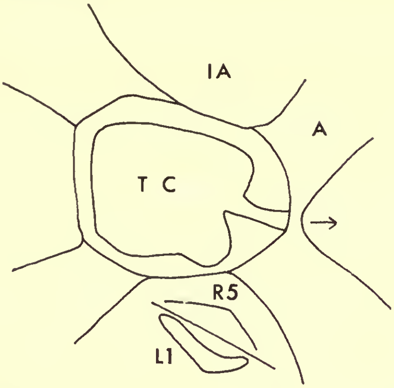


FIG. 13. *Staurocystis quadrifasciatus* (Pearce). Sketch of apical region ground down. Note embayment above rhomb L1 : R5 at position of gonopore and hydropore. A, ambulacrum ; IA, inter-ambulacrum ; TC, thecal cavity. The arrow points to the periproct. BMNH. 57381.

distal portions (see Pl. 10, figs. 1, 4, 5). The proximal portion tapers rapidly and the outer proximals have a smooth external flange. The distal portion is almost without any taper and the alternation of the distals is indistinct after the first few pairs. BMNH. E.7553, 38696 and BU. H019 show distinct branched root structures.

REMARKS. This is the commonest species from the Wenlock Limestone and was gregarious. A slab of Wenlock Limestone in the Geological Survey & Museum, London, has the remains of 8 specimens preserved on it and one in the Dudley Library has remains of 10 specimens. Another slab, in the Sedgwick Museum, has 2 specimens of this species and one of *Tetracystis oblongus* (Forbes) on it. It is interesting that despite the complexity of the food collecting apparatus in this genus, it is confined to the Wenlock Limestone, whereas *Tetracystis* and *Pseudocrinites* are more widely distributed and survived until the Devonian.

Genus ***PSEUDOCRINITES*** Pearce 1843

TYPE SPECIES. *Pseudocrinites bifasciatus* Pearce 1843, by designation of Haeckel (1896*a* : 135).

DIAGNOSIS. A genus of Staurocystinae with lens-like, biconvex theca ; with two ambulacra. Modified from Kesling (1963 : 111).

Ten species of *Pseudocrinites* have so far been described in addition to the one Schuchert described as *Trimerocystis peculiaris*, an abnormal individual which had three ambulacra instead of the usual two. Kesling (1961*a* : 257) considered *P. abnormalis* Schuchert and *T. peculiaris* Schuchert to be synonymous with *Pseudocrinites gordoni* Schuchert, and I believe that *Pseudocrinites magnificus* Forbes is probably a very large individual of *P. bifasciatus* Pearce. This reduces the number of species to 8 and it might be possible to reduce it even further if a comprehensive study of the American species were undertaken. One new species is described here based on two specimens from the Holcroft collection (BU). Both differ considerably from *P. bifasciatus* but quite closely resemble the American species *P. perdewi* Schuchert.

Regional distribution. England : Dudley, Walsall, Sedgley. United States : W. Virginia, Pennsylvania and Maryland.

Stratigraphic range. Wenlock Limestone (Middle Silurian) to Manlius Formation (Devonian, Gedinnian).

Pseudocrinites bifasciatus Pearce

(Pl. 2, figs. 4–8 ; Pl. 3, figs. 2–6 ; Pl. 10, figs. 7, 8 ; Text-figs. 14–19)

1843*a* *Pseudocrinites bifasciatus* Pearce : 160.
1843*b* *Pseudocrinites bifasciatus* Pearce : 472.
1843*c* *Pseudocrinites bifasciatus* Pearce : 265.
1844 *Pseudocrinites bicopuladigiti* Garner : 160, pl. A, figs. 8–13.
1848 *Pseudocrinites bifasciatus* Pearce ; Forbes : 496, pl. 11, figs. 1–7.
1848 *Pseudocrinites magnificus* Forbes : 497, pl. 12, figs. 1–4.
1854 *Pseudocrinites bifasciatus* Pearce ; Murchison : 216.
1854 *Pseudocrinites magnificus* Forbes ; Murchison : 216, text-fig. 37, fig. 1.
1857 *Pseudocrinus bifasciatus* (Pearce) Pictet ; 298, pl. 99, fig. 12.
1857 *Pseudocrinus magnificus* (Forbes) Pictet : 298.
1867 *Pseudocrinites bifasciatus* Pearce ; Murchison : 222, 513.
1867 *Pseudocrinites magnificus* Forbes ; Murchison : 222, 513, text-fig. 55, fig. 1.
1868 *Pseudocrinites bicopuladigiti* Garner ; Bigsby : 26.
1868 *Pseudocrinites bifasciatus* Pearce ; Bigsby : 26.
1868 *Pseudocrinites magnificus* Forbes ; Bigsby : 26.
1873 *Pseudocrinites bifasciatus* Pearce ; Salter : 127, 2 figs.
1876 *Pseudocrinites bifasciatus* Pearce ; Quenstedt : 678, pl. 113, figs. 74 (3 figs.), 75.
1891 *Lepadocrinus bifasciatus* (Pearce) Woods : 43.
1891 *Pseudocrinus bifasciatus* (Pearce) ; Carpenter : 7, 10.
1895 *Pseudocrinus bifasciatus* (Pearce) ; Bernard : 206, text-fig. 73*c*.
?1896 *Pseudocrinus*, Haeckel : 401.
1896*a* *Pseudocrinites bifasciatus* Pearce ; Haeckel : 135, pl. 3, figs. 25, 26.
1896*a* *Pseudocrinites magnificus* Forbes ; Haeckel : 136.
1899 *Pseudocrinites bifasciatus* Pearce ; Jaekel : 285, pl. 14, fig. 3, text-fig. 60.
1899 *Pseudocrinites magnificus* Forbes ; Jaekel : 285, pl. 14, fig. 4.
1900 *Pseudocrinus* Bather : 62, text-fig. 29.
1904 *Pseudocrinites bifasciatus* Pearce ; Schuchert : 227, 229.
1904 *Pseudocrinites magnificus* Forbes ; Schuchert : 229.
1943 *Pseudocrinites bifasciatus* Pearce ; Bassler & Moodey : 53, 185.
1943 *Pseudocrinites magnificus* Forbes ; Bassler & Moodey : 53, 185.

Diagnosis. A *Pseudocrinites* with circular outline to theca ; very broad ambulacra reaching stem ; periproct composed of anal pyramid and complete circlet of auxiliaries ; thecal plates sculptured with coarse irregular ridges giving theca a malleated appearance.

Holotype. Pearce's original specimen (Bristol Museum Ca.7862) was destroyed in an air-raid on 24th November, 1940. Again as this species is readily recognized and there is no point of taxonomy to be settled no neotype is designated.

Material. About 35 specimens in BMNH., BU., DL., GSM., OUM., RSM., SM.

Horizon and locality. Wenlock Limestone, Middle Silurian ; Dudley (Wren's Nest and Castle Hill).

Before describing the species it is necessary to settle the synonymy between *P. bifasciatus* Pearce and *P. magnificus* Forbes.

There is a constant number of brachioles per unit length in the ambulacra of *Staurocystis quadrifasciatus* and, according to Kesling (1961*a*), in *Pseudocrinites gordoni* Schuchert. If this holds true for *P. bifasciatus* there will be a linear relationship between thecal diameter and the total number of brachioles. Text-fig. 14 clearly shows that this is so and that *P. magnificus* falls very close to the predicted value for a large *P. bifasciatus*. This is a particularly important point for in his original description Forbes (1848 : 497) stated that " the arms extend completely down the sides, and are remarkable for the great number of fingers [brachioles] on each, being no fewer than 34. [Forbes only counted the brachioles on one side of each ambulacrum.] They are much more closely packed, longer, slenderer, and apparently more flexible than in the last species. [*P. bifasciatus*] ". The number of brachioles was the main point distinguishing the two species and since there is in fact very little real difference they must be considered synonymous.

Description. The theca is circular in outline, biconvex and lens-like. There are two ambulacra running around the periphery of the theca and usually reaching the

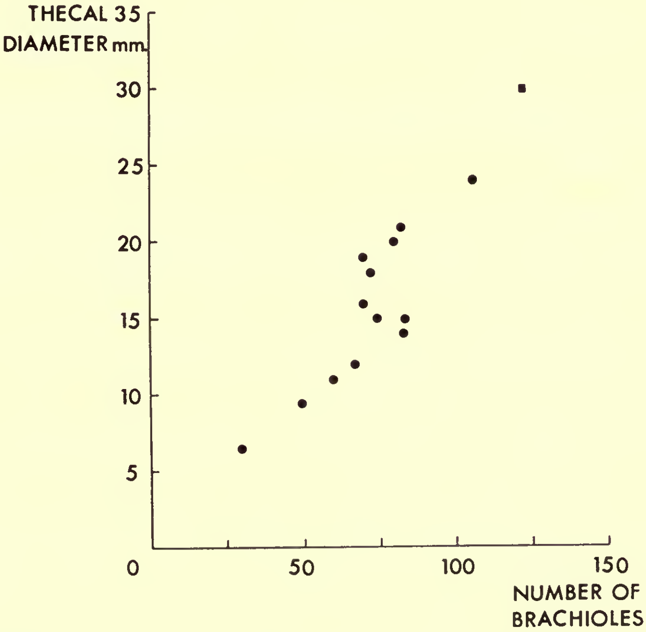


Fig. 14. Graphical representation of relationship between diameter and total number of brachioles in *Pseudocrinites bifasciatus* Pearce and *P. magnificus* Forbes. The square dot represents the holotype of *P. magnificus*.

stem. The mouth, gonopore and hydropore are apical and the anus lateral. The anus and rhomb L4 : R3 were in one lateral face, the periproctal face, while rhombs B2 : IL2 and L1 : R5 were in the other face. The gonopore and hydropore are therefore in this face which is referred to as the gonal face.

The thecal plates of the first four circlets are arranged in the usual order (see Text-fig. 15). The exact positions of the ambulacra may vary slightly but otherwise there is very little variation. As far as it is possible to determine the arrangement of the visible portions of the orals is as in Text-fig. 16 but they extended over a larger area beneath the ambulacra. The four basals combine abapically to form an oval cicatrix 5·5 mm. by 5·0 mm. in SM. A12593. All the plates are ornamented with irregular and discontinuous radiating and concentric ridges very much like those of *Staurocystis*. The portions of the thecal plates underlying the ambulacra bear the impressions of the flooring plates. These are much less closely packed than in *Staurocystis* (see Text-fig. 18).

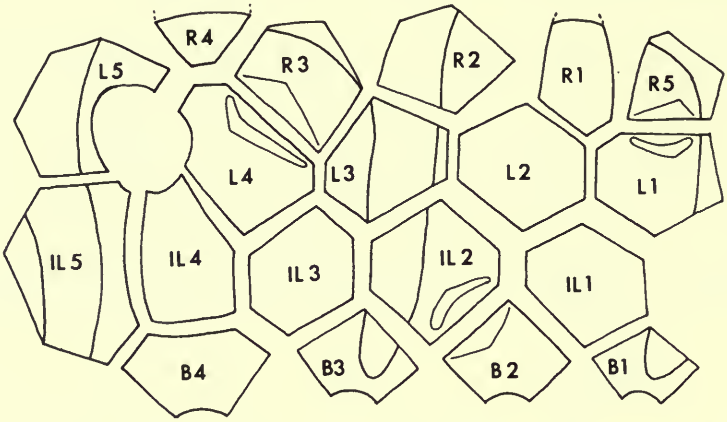


FIG. 15. *Pseudocrinites bifasciatus* Pearce. Sketch of arrangement of thecal plates of first four circlets. BB, basals; ILL, infra-laterals; LL, laterals; RR, radials. Based on specimen SM. A.12593.

Three disjunct pectinirhombs are present, of these B2 : IL2 and L1 : R5 are about the same size and L4 : R3 is distinctly larger.

B2 : IL2. (SM. A12593). This rhomb is depressed, angular and almost perfectly symmetrical. It measures 4·7 mm. by 3·8 mm. externally and has 22 dichopores in a width of 3·9 mm., the longest reaching 3·0 mm. The slits in B2 are 0·07 mm. wide and separated by 0·125 mm. They reach a maximum length adaxially of 0·87 mm. Those in IL2 are 0·107 mm. wide and separated by 0·09 mm. and reach a maximum length of 0·62 mm. The closed rim on IL2 protrudes about 0·4 mm. from the general surface of the plate.

L1 : R5. (SM. A10192). This rhomb is depressed, more or less equal and symmetrical. It measures 4·35 mm. by 3·65 mm. externally and has 20 dichopores in a width of 3·35 mm., the longest reaching approximately 3·0 mm. The slits in R5 are

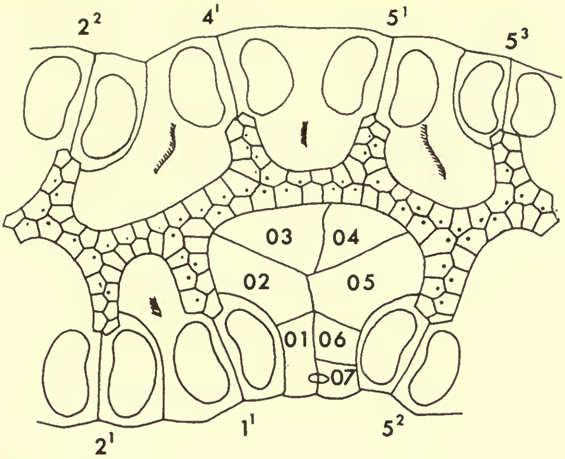
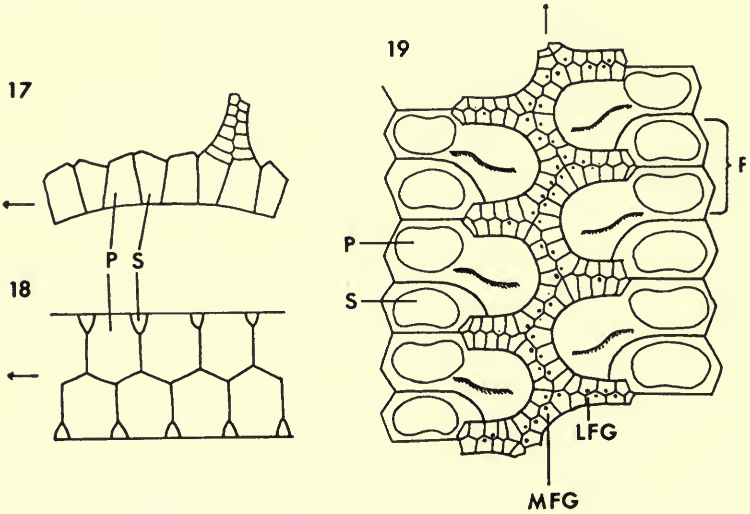


FIG. 16. *Pseudocrinites bifasciatus* Pearce. Sketch of apical region, showing arrangement of the ambulacra, interpretation of the brachioles and the exposed portions of the oral plates. OO, orals. SM. A.10192.

0·07 mm. wide and separated by 0·125 mm. The longest reaches 1·1 mm. Unfortunately the slits in L1 are obscured by matrix but could not have exceeded 0·65 mm. in length. L1 has a closed rim extending about 0·4 mm. from the level of the plate surface.

L4 : R3. (SM. A12593). This is depressed, very asymmetrical and angular. It measures 6·0 mm. by 3·0 mm. approximately (it is slightly damaged). There are 32 dichopores in a width of 6·0 mm. and the longest reaches approximately 2·35 mm. The slits in R3 are 0·07 mm. wide and separated by 0·125 mm., the longest reaching 0·87 mm. Again unfortunately those in L4 are obscured by matrix but could not have exceeded 0·53 mm. in length.

The mouth lay apically between facets 4^1 and 1^1 and shows as a narrow curved slit in BMNH. 47833. This specimen shows the internal view of the gonal face and apex. There is a slight groove internally in R5 below the gonopore and the hydropore. There are two broad ambulacra which coalesce at the apex and usually reach the stem. They are 5 mm. wide at the apex in SM. A12593 and taper gradually to about 3 mm. at their rounded tips. The primary flooring plates are not as thin as those of *Staurocystis* resulting in a more distant spacing of the brachioles. The ambulacra are more prominent than in *Staurocystis* and reach a height of 2 mm. in BMNH. 40189. The brachiole facets are kidney-shaped areas which are quite prominent and set at an angle of about 45 degrees to the line of the ambulacrum. The spacing of the facets appears to be constant throughout growth and a specific character. The average of ten measurements was 4 brachioles in 5·3 mm. with maximum and minimum of 4 in 6·0 mm. and 4 in 4·9 mm. These measurements were taken from thecae varying in diameter from 11 mm. to 24 mm. The main and lateral food grooves of the ambulacra are provided with cover plates which are much broader than those of *Staurocystis* or *Pseudocrinites pyriformis* sp. nov. and are frequently ornamented with tubercles (see Text-fig. 19). Apparently these cover plates formed a permanent roof over the food grooves. Between lateral food grooves the primary flooring plates are ornamented with a slightly sinuous ridge. The brachioles taper very rapidly near the base so that although the facets are almost in contact adjacent brachioles are widely separated. They are composed of about 24 to 28 brachiolars and reach a length of about 6–6·5 mm. Basally they are 1 mm. wide and taper rapidly to start with, then gradually to about 0·5 mm. at the tips. The brachioles are provided with cover plates which are 3 or 4 times as numerous as the brachiolars. Most of these features are well preserved on BMNH. E.29068.



Figs. 17–19 *Pseudocrinites bifasciatus* Pearce. Fig. 17. Sketch of side of an ambulacrum, showing primary and secondary flooring plates and a brachiole tapering rapidly at the base. Fig. 18. Sketch of impression of ambulacral flooring plates on the thecal plates. Fig. 19. Sketch of part of an ambulacrum. F, facet ; LFG, lateral food groove ; MFG, main food groove ; P, primary flooring plate ; S, secondary flooring plate. The arrows point to the mouth. Based on specimen SM. A.10192.

The periproct is surrounded by four plates. In increasing order of contribution to the border these are : IL5, IL4, L4, L5, the latter contributing about one-third the total. There is no periproct hood in L5. The periproct is covered by an anal pyramid, composed of 5 or 6 anals and up to 2·65 mm. in diameter, and an auxiliary circlet which is always complete and composed of 10 plates in BMNH. E.29068 and 40198. Both anals and auxiliaries are apparently unornamented.

The gonopore and hydropore are apical and shared by O1 and O7. The gonopore is a small circular opening 0·25 mm. in diameter in BU. Ho12 which is a very immature specimen. The hydropore is oblong in this specimen and about twice the size of the gonopore. No gonals have been observed. As previously mentioned, there is a groove in R5, which corresponds in position to the embayment seen in *Staurocystis*, below the position of these two orifices.

The stem is composed of the usual proximal and distal portions and, in BMNH. 40189, has a root structure. The outer proximals are provided with a smooth external flange and the distals are not clearly recognizable as large and small throughout most of the length. In BMNH. 40189 there are 14 outer proximals and about 21 distals of which the first six are in distinct pairs of large and small. The stem is about 27 mm. long.

REMARKS. Schuchert (1904 : 228–229) grouped the American species of this genus into three groups :

P. gordoni group. Thecal outline circular, ambulacra reaching the stem, auxiliary circlet complete.

P. clarki group. Thecal outline elongate, ambulacra reaching the stem, auxiliary circlet incomplete.

P. perdewi group. Thecal outline pyriform, ambulacra not reaching the stem, auxiliary circlet complete.

Schuchert assigned *P. bifasciatus* and *P. magnificus* to the *gordoni* group and this seems to be correct. However, some doubt may be cast as to the distinctness of the first two groups as some examples of *P. bifasciatus* seem to have elongate thecae, and the nature of the auxiliary circlet is known to vary within a single species in other genera of Staurocystinae. The third group, that of *P. perdewi*, is apparently quite distinct from the other two and the next species described in this paper belongs in it. There may be some grounds for separating these two species from the others subgenerically but without a thorough re-examination of the American species this would seem a hasty action.

Pseudocrinites pyriformis sp. nov.

(Pl. 3, figs. 1, 7 ; Pl. 4, figs. 1–5 ; Pl. 5, fig. 1 ; Text-figs. 20, 21)

DIAGNOSIS. A *Pseudocrinites* with pyriform outline to the theca ; broad ambulacra extending only half way down the sides ; thecal plates showing coarse irregular sculpture adorally and fine irregular sculpture associated with fine radiating ridges aborally.

HOLOTYPE. BU. H010.

MATERIAL. In addition to the holotype, paratype BU. H011.

HORIZON and LOCALITY. Sedgley (Aymestry) Limestone, Upper Silurian ; Sedgley, Staffs.

DESCRIPTION. The theca is pyriform in outline and bilaterally compressed with ambulacra in a broad band running across the top of the theca and extending about half way down the sides. The mouth, gonopore and hydropore are apical and the anus lateral. Rhombs B2 : IL2 and L1 : R5 are in the gonal face, and the periproct and rhomb L4 : R3 in the periproctal face. The theca was provided with a stem.

The arrangement of the thecal plates of the first four circlets is as in Text-fig. 20. The arrangement of the orals is unknown. Neither of the specimens available shows all the thecal plates, and those plates shown in dashed outline are not clearly visible.

In BU. Ho11 the ambulacra extend a little further down the theca and encroach upon ILL2 and 5, but this seems to be the only difference. Where the plates are not covered by the ambulacra they have a very distinctive ornament. In the adoral half of the theca this is of very irregular ridges and pits accompanied by fine tubercles throughout. Aborally however the ornament is of much finer irregular ridges, which do not protrude as far from the general surface, fine tubercles and some fine radiating ridges. In the holotype the basal plates appear to be almost smooth but this is partly due to weathering. The basals unite abapically to form a cicatrix 7·3 mm. by 6·0 mm., but as this part of the theca is slightly crushed the cicatrix may have been circular originally.

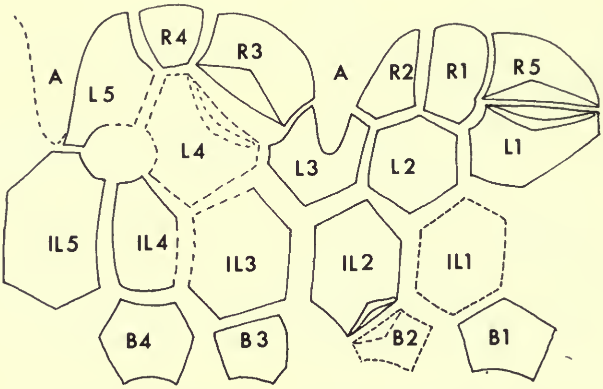


FIG. 20. *Pseudocrinites pyriformis* sp. nov. Sketch of arrangement of thecal plates of first four circlets. AA, ambulacra ; BB, basals ; ILL, infra-laterals ; LL, laterals ; RR, radials. The plates indicated by a dashed outline are not clearly visible. Based on specimen BU. Ho10.

The usual three disjunct pectinirhombs are developed. Both specimens show L1 : R5 clearly, the holotype shows half-rhomb R3, and neither show B2 : IL2 clearly although part of it is visible.

B2 : IL2. Part of IL2 shows in the holotype. It has a closed rim and shows 18 slits in a width of 4·2 mm., the longest reaching 1·0 mm. The slits are 0·161 mm. wide and separated by 0·107 mm. which is unusually wide.

L1 : R5. (Holotype). This is very depressed, more or less angular and symmetrical. It measures 12·3 mm. by 5·7 mm. externally and has 43 dichopores in a width of 11·7 mm., the longest reaching 4·0 mm. The slits in R5 are 0·107 mm. wide and separated by 0·125 mm. They reach a length of 2·0 mm. Those in L1 are 0·143 mm. wide and separated by 0·09 mm. They reach a maximum length adaxially of 0·95 mm. Due to the development of the closed rim around this half-rhomb these slits open on a surface sloping away from the suture at an angle approaching 45 degrees (see Pl. 4, fig. 2).

(BU. Ho11). This rhomb is much the same and has about 40 dichopores in a width of 12 mm. approximately. The slits in R5 reach a length of 2·0 mm. while those in L1 reach 1·0 mm. The slits are again narrower, and consequently more widely separated, in R5 than in L1.

L4 : R3. (Holotype). This rhomb is only half visible and shows 45 dichopores in R3 in a width of 12·0 mm. but there were probably a few more which are now hidden by matrix. It is asymmetrical, there being 18 dichopores in the demi-rhomb adjacent to the periproct and therefore at least 27 in the other demi-rhomb. The slits in R3 are 0·107 mm. wide and separated by 0·125 mm. The longest is 2·33 mm. long.

The mouth has not been directly observed but presumably lay between facets 1^1 and 4^1 as in *P. bifasciatus*. The ambulacra are developed on broad bands which taper relatively rapidly. They are 7 mm. wide apically and taper to about half that just before their rounded tips. Apically the ambulacral flooring plates are 3·5 mm. high in the holotype and 4·0 mm. in Ho11. There are 14 facets in ambulacrum 5 and 16 in ambulacrum 2 of Ho10, the corresponding figures for Ho11 being 20 and 24. The arrangement of the flooring plates is much the same as in *P. bifasciatus* but the brachioles are much more widely spaced. The average of four measurements was 4 facets in 10·4 mm. with maximum and minimum distances of 10·0 and 11·0 mm. These are almost twice the distances for *P. bifasciatus*. The facets are large kidney-shaped areas which are almost planar. The main and lateral food grooves are provided with highly ornamented cover plates which are relatively long and narrow. They have the same general proportions as those of *Staurocystis* but differ in being much larger and in being covered with strongly raised ridges. Between the lateral food grooves the primary flooring plates are highly ornamented with raised tubercles, and both types of flooring plates are ornamented with ridges laterally. The main food grooves are provided with a narrow ledge on which the cover plates rested in life. The lateral food grooves were relatively short. The brachioles are composed of alternating brachiolars ornamented with tubercles and ridges. The penultimate

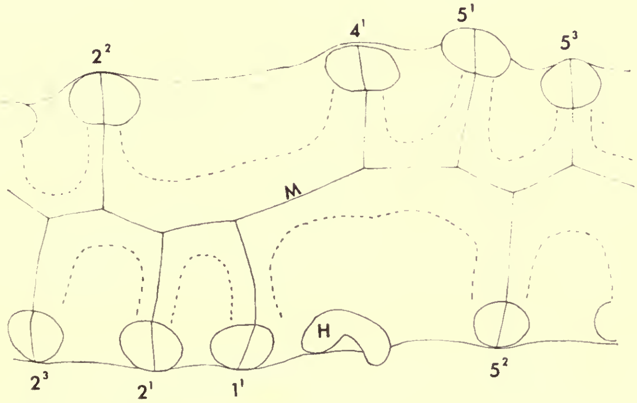


FIG. 21. *Pseudocrinites pyriformis* sp. nov. Camera lucida drawing of apical region. H, hydropore ; M, approximate position of mouth. Cf. Text-figs. 4, 16. Based on specimen BU. Ho10.

brachiole in ambulacrum 5 of Ho11 is 9·35 mm. long and has 22 brachiolars in this distance. It is incomplete however. The terminal brachiole apparently exceeds 12 mm. in length and this too is incomplete. The penultimate one tapers from 1·45 mm. wide at the base to 0·65 mm. where it is broken off. The cover plates are apparently ridged and about 2–3 per brachiolar.

The periproct is probably surrounded by four plates but cannot be seen completely in either specimen. Parts of the anal pyramid and auxiliary circlet can be made out in the holotype but the total number of plates in each is unknown. In Ho11 the auxiliaries were ornamented with ridges. There is no periproct hood in L5.

The gonopore and hydropore lay apically presumably across the common suture of O1 and O7. The gonopore is small, circular and provided with a pyramid of gonals, of which 2 can be seen in the holotype. It is 0·35 mm. wide in the holotype and 0·65 mm. wide in Ho11. The hydropore is curved around the gonopore adapically and provided with a conspicuous rim bearing ridges externally. It is 1·85 mm. wide in the holotype and 3·45 mm. wide in Ho11.

21·5 mm. of the proximal stem is preserved in the holotype. It tapers from 7·0 mm. to 4·5 mm. in this distance and there are 26 outer proximals each provided with an external flange that has tubercles developed on the less weathered portions.

REMARKS. This species is quite distinct from the preceding but closely resembles *P. perdewi* Schuchert. It differs from the latter species in the brachiole and dichopore spacing, in having more prominent ambulacra and less prominent rhombs. The holotype has 45 dichopores in L4 : R3 whereas a specimen of *P. perdewi* of about the same dimensions would have about 70 dichopores in the same rhomb. The ornamentation of the plates of the two species is also quite different. As a general rule the British species of Staurocystinae seem to have more prominent ambulacra and less well developed rhombs than their American counterparts.

Genus ***TETRACYSTIS*** Schuchert 1904

TYPE SPECIES. *Tetracystis chrysalis* Schuchert 1904.

DIAGNOSIS. A genus of Staurocystinae with four protruding ambulacra all reaching the stem ; relatively widely spaced brachioles ; wide main food groove and short lateral food grooves ; some secondary ambulacral flooring plates reaching ambulacral mid-suture ; ambulacral cover plates rarely preserved.

Hitherto the genus *Tetracystis* has been assigned to the subfamily Apiocystitinae. Kesling (1963 : 108) lists among the characters of the Staurocystinae that the ambulacra are strongly protuberant. In both genera attributed by Kesling to the Staurocystinae this is due to the ambulacra being developed on smooth bands on the thecal plates and not in shallow grooves as in the Apiocystitinae. In both these respects *Tetracystis* resembles *Staurocystis* and *Pseudocrinites* and is therefore included in the Staurocystinae.

The specimens described by Forbes as *Pseudocrinites oblongus* apparently belong to this genus. They have four ambulacra three pectinirhombs and four plates bordering the periproct. In Regnéll's scheme for the Apiocystitinae (Regnéll

1945 : 91) there are only three genera which fall into this category. These are *Lovenicystis* Regnéll 1945, *Jaekelocystis* Schuchert 1903 and *Tetracystis* Schuchert 1904. The present specimens differ from *Lovenicystis* in having all the ambulacra reaching the column and from *Jaekelocystis* in having angular pectinirhombs in which one half-rhomb is not reduced to a spout-like pore. They agree with *Tetracystis* in these respects and also in the nature of the ambulacra which has caused their removal to the Staurocystinae. There are only three other species known at present, *T. chrysalis* Schuchert, *T. bifarius* Amsden and *T. fenestratus* (Troost). The British species appears to differ from all three in having more prominent ambulacra.

REGIONAL DISTRIBUTION. England: Dudley; United States: Tennessee and W. Virginia.

STRATIGRAPHICAL RANGE. Middle Silurian to Basal Devonian.

Tetracystis oblongus (Forbes) 1848

(Pl. 5, figs. 2–7, 11–13; Pl. 10, figs. 6, 13; Text-figs. 22–25)

1848 *Pseudocrinites oblongus* Forbes : 499, pl. 14, figs. 1–14.
1854 *Pseudocrinites oblongus* Forbes ; Murchison : 217.
1857 *Pseudocrinus oblongus* (Forbes) Pictet : 298.
1867 *Pseudocrinites oblongus* Forbes ; Murchison : 222, 513.
1868 *Pseudocrinites oblongus* Forbes ; Bigsby : 26.
1873 *Pseudocrinites oblongus* Forbes ; Salter : 127.
1876 *Pseudocrinites oblongus* Forbes ; Quenstedt, pl. 113, fig. 79, (3 figs.).
1891 *Pseudocrinus oblongus* (Forbes) ; Carpenter : 10.
1896*a* *Staurocystis oblongus* (Forbes) Haeckel : 134.
1899 *Apiocystites oblongus* (Forbes) Jaekel : 282.
1900 *Lepadocrinus oblongus* (Forbes) Bather : 62.
1943 *Lepocrinites oblongus* (Forbes) Bassler & Moodey : 52, 173.

DIAGNOSIS. A *Tetracystis* with broad, prominent ambulacra; up to 30 brachioles per ambulacrum and up to 30 dichopores per rhomb; periproct relatively depressed.

LECTOTYPE. Forbes did not designate a type but the specimens he examined were in the Fletcher and Gray collections. Among the specimens in the Fletcher collection is the original of Forbes' pl. 14, fig. 1 (SM. A10140), here selected as lectotype.

MATERIAL. In addition to the lectotype, 9 specimens in BMNH. GSM., SM.

HORIZON AND LOCALITY. Wenlock Limestone, Middle Silurian; Dudley, Worcs.

DESCRIPTION. The theca is subquadrate with four ambulacra reaching the stem. The mouth, gonopore and hydropore are apical and the anus lateral. No complete stem has been seen.

The arrangement of the thecal plates of the first four circlets is shown in Text-fig. 22. Very few specimens are known and there is little variation among them. The four basal plates unite abapically to form a circular cicatrix 4 mm. in diameter in the lectotype. The thecal plates are ornamented with irregular radiating and concentric ridges which are often discontinuous and strongly resemble the ornamentation in *Staurocystis* and *Pseudocrinites bifasciatus*. Beneath the ambulacra the traces of the

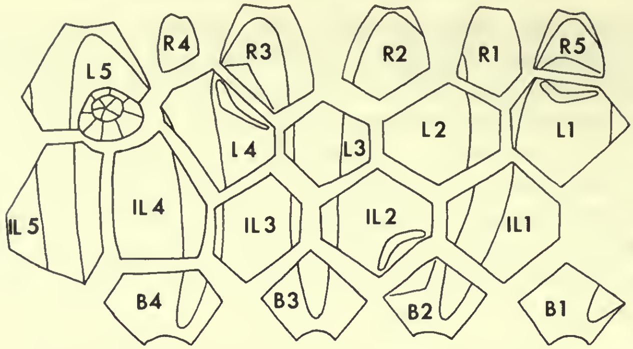
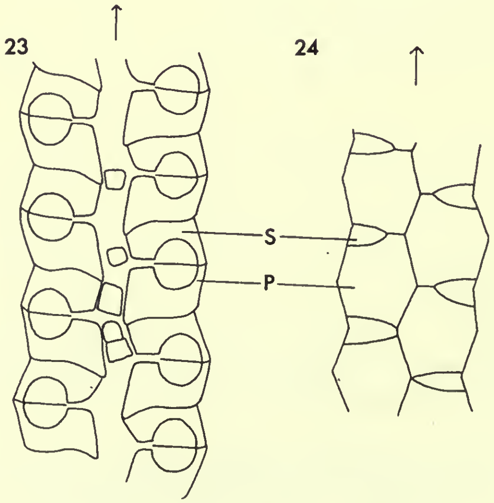


FIG. 22. *Tetracystis oblongus* (Forbes). Sketch of arrangement of thecal plates of first four circlets. BB, basals; ILL, infra-laterals; LL, laterals; RR, radials. Based on specimen SM. A.10140.

ambulacral flooring plates can be made out. As far as can be determined from BMNH. 57411 there were 7 orals arranged in much the same way as in *Staurocystis*.

The usual three disjunct pectinirhombs are present. They are all angular and depressed in outline.

B2 : IL2 (Lectotype). This is 3·15 mm. by 2·15 mm. and has 19 dichopores in a width of 2·9 mm. The longest dichopore is 1·8 mm. The slits in IL2 are obscured by matrix, those in B2 are up to 0·054 mm. wide and separated by 0·125 mm. IL2 is provided with a closed rim.



FIGS. 23, 24. *Tetracystis oblongus* (Forbes). Fig. 23. Sketch of part of an abulacrum. Fig. 24. Sketch of impression of ambulacral flooring plates on the thecal plates. P, primary flooring plate; S, secondary flooring plate. The arrows point to the mouth. Based on specimen SM. A.10140.

L1 : R5 (Lectotype). This is 3·75 mm. by 2·75 mm. externally and has 23 dichopores in a width of 3·6 mm. and the longest dichopore is 2·27 mm. The slits in both half-rhombs are 0·07 mm. wide, and separated by 0·125 mm. Those of L1 reach 0·54 mm. in length while those in R5 reach 1·0 mm.

L4 : R3 (Lectotype). The rhomb measures 4·8 mm. by 3·0 mm. and is asymmetrical, possibly due to the proximity of ambulacrum 4. There are 28 dichopores, all of which are disjunct, in a width of 4·45 mm. and the longest is 2·4 mm. The slits in L4 are 0·07 mm. wide and separated by 0·107 mm. while those the longest reaching 0·67 mm. Those in R3 are only 0·055–0·06 mm. wide and separated by 0·1 mm. The longest is 0·95 mm. long.

The mouth was apical and slit-like (BMNH. 57411) and apparently surrounded by 7 orals. The four ambulacra meet in the oral area and the first formed facets are on the left as in other species of Staurocystinae (see Text-fig. 25). The four ambulacra are developed on relatively narrow bands which, contrary to Forbes' statement, hardly taper at all. They are 2·5 mm. wide apically and still 2·0 mm. wide near their tips. They are much more conspicuous in this species than in the American species. The arrangement of the ambulacral flooring plates is shown in Text-fig. 24. The secondary flooring plates are much larger relatively than in *Staurocystis* or *Pseudocrinites* and quite frequently reach the ambulacral mid line. The brachiole facets are rather inconspicuous but slightly raised and the lateral food grooves are relatively short. Both the lateral and main food grooves were covered with ambulacral cover plates which were subquadrate and unornamented. Apparently the primary flooring plates were also unornamented between the lateral food grooves. The spacing of the brachiole facets varies within much wider limits than in the previous two genera. The average of 8 measurements was 4 brachioles in 5·73 mm. but varied from 4 in 4·67 mm. to 4 in 7·0 mm. This may vary within a single specimen and is not directly associated with growth as the largest theca had an intermediate value. The brachioles are narrow, being 0·7 mm. wide basally in SM. A12603, and they taper gradually. No complete brachiole has been seen but 20 brachiolars are preserved in some brachioles on SM. A12603.

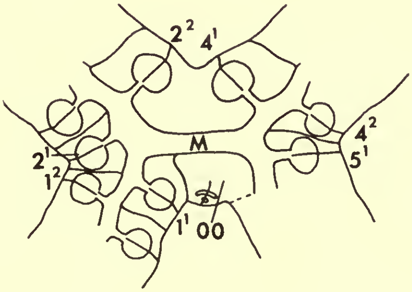


FIG. 25. *Tetracystis oblongus* (Forbes). Sketch of apical region of theca. M, approximate position of mouth ; OO, position of exposed portions of some of the oral plates. Based on specimen SM. A.10140.

The periproct is surrounded by four plates, which are in increasing order of contribution to the border; L4, IL4, IL5, L5. L4 only just reaches the periproct as in some examples of *Staurocystis*. There is no periproct hood in L5. The periproct consists of an anal pyramid of 5 or 6 anals surrounded by a closed circlet of auxiliaries. These are unequally developed so the border of the anal pyramid is narrower adapically as shown in Text fig. 22. There were 9 or 10 auxiliaries in the lectotype and probably more in BMNH. E.29075. Both types of plate may have been slightly ornamented with irregular ridges.

The gonopore and hydropore are apical, presumably developed across the suture between OO1 and 7. Both are inconspicuous and it is impossible to confirm the multiple perforations of the gonopore described by Schuchert (1904).

No complete stem has been seen so it is impossible to confirm that a root structure was developed but this seems likely. SM. A12603 has 10 outer proximals preserved. All have a smooth external flange.

Genus ***PRUNOCYSTITES*** Forbes 1848

Type species. *Prunocystites fletcheri* Forbes 1848.

Diagnosis. A genus of Staurocystinae with (probably 4) short ambulacra confined to apex of theca; with few relatively long and slender brachioles.

This genus was erected by Forbes to contain the single species *P. fletcheri*, of which at the time only the holotype (SM. A10187) was available. The genus was therefore based on this single specimen which is partly buried in matrix and hence, as Forbes stated (1848 : 503), the original description was imperfect. The holotype, and all subsequently found specimens, are small and it is difficult to assess whether they are immature or adult and, if they are immature, which characters are the result of immaturity. Only one of the specimens available is isolated from the matrix and this has several plates obscured. If all the available specimens are conspecific it is possible to build a composite picture of the characters of the genus, but it must be emphasized that this picture is composite.

Forbes (1848 : 503–504) did not discuss the affinities of *P. fletcheri* but later (1848 : 526) he placed it in a position intermediate between *Echinoencrinites* s.l. and *Pseudocrinites* s.l. which roughly correspond to the Echinoencrinitidae and Staurocystinae. Jaekel (1899) considered *P. fletcheri* and "*Echinoencrinites*" *baccatus* Forbes to be congeneric and therefore assigned the latter to *Prunocystites*, and both species to his family Scoliocystidae (=Echinoencrinitidae). This course has been accepted subsequently. "*E.*" *baccatus* is commoner than *P. fletcheri* and its characters are better known. The concept of *Prunocystites* has therefore been partly based on this species which undoubtedly belongs in the Echinoencrinitidae s.l., where it was placed by Forbes. This accounts for *Prunocystites* having been considered as an echinoencrinitid.

P. fletcheri differs from all other British Callocystitids in having ambulacra confined to the apex of the theca but this could be the result of the small size (? and immaturity) of the thecae known. If the specimen figured in Pl. 9, fig. 10 is really *P. fletcheri* it would indicate that this is a feature of immaturity. The staurocystinid type of ambulacrum can be confirmed in the holotype of *P. fletcheri* if it is wetted with alcohol and examined under a fairly high magnification. On this evidence the genus *Prunocystites* is transferred to the Staurocystinae. There emerges the possibility that all or some of the thecae grouped under *P. fletcheri* are young specimens of other staurocystinid species. They are not young of *Pseudocrinites bifasciatus* which are well known and easily recognized. The long, slender and relatively widely spaced brachioles would seem to preclude *Staurocystis quadrifasciatus* and *Tetracystis oblongus* but young specimens of these species are apparently unknown.

In view of the general uncertainty about *Prunocystites* it is suggested that the name be retained for the specimens described below until such time as it may become possible to settle the characters and affinities of the genus. This leaves "*E.*" *baccatus* Forbes without a genus and, as there is no other name available, the genus *Glansicystis* nov. (*glans* = acorn) is proposed for it (see p. 344).

Prunocystites fletcheri Forbes

(Pl. 3, figs. 8, 9; Pl. 8, fig. 4; Pl. 9, fig. 11, ?10; Text-figs. 26–29)

1848 *Prunocystites fletcheri* Forbes : 504, pl. 16, figs. 1–4.
1854 *Prunocystites fletcheri* Forbes ; Murchison : 217, text-fig. 37, fig. 3.
1857 *Prunocystites fletcheri* Forbes ; Pictet : 299, pl. 99, fig. 16 (2 figs.).
1867 *Prunocystites fletcheri* Forbes ; Murchison : 222, text-fig. 55, fig. 3.
1868 *Prunocystites fletcheri* Forbes ; Bigsby : 26.
1873 *Prunocystites fletcheri* Forbes ; Salter : 127.
1876 *Prunocystites fletscheri* (sic) Forbes ; Quenstedt : 685, pl. 113, fig. 90.
1891 *Prunocystites fletcheri* Forbes ; Woods : 43.
1899 *Prunocystites fletscheri* (sic) Forbes ; Jaekel : 282.
1900 *Prunocystites fletcheri* Forbes ; Bather : 60, text-fig. 24.
1943 *Prunocystites fletcheri* Forbes ; Bassler & Moodey : 53, 185.

DIAGNOSIS. As for the genus.

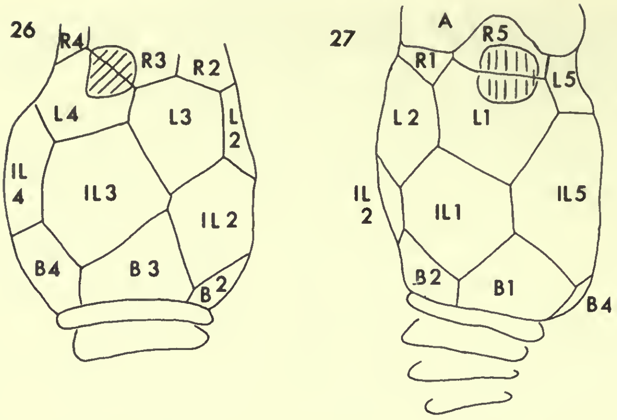
HOLOTYPE. SM. A10187.

MATERIAL. BMNH. 40207, 57395–96 ; DL. 307 ; SM. A.10187–88, A.12579 ; ?BU. IVa.25.

HORIZON AND LOCALITY. Wenlock Limestone, Middle Silurian ; Dudley, Worcs.

DESCRIPTION. The theca is ovate and very small, being only 5 mm. high in the holotype. The brachioles are developed apically on short ambulacra that protrude from the theca. The mouth was presumably apical, the anus lateral and high up on the theca. The gonopore and hydropore are unknown. In all but one theca there are only two rhombs, B2 : IL2 being undeveloped. The proximal stem is nearly as wide as the theca in some cases, tapers rapidly and is very short. The distal stem in SM. A10188 is very long and slender.

The thecal plates are arranged in a definite order and although it has not been possible to confirm the complete arrangement in any one specimen a composite picture may be built up from the specimens available. This composite picture suggests

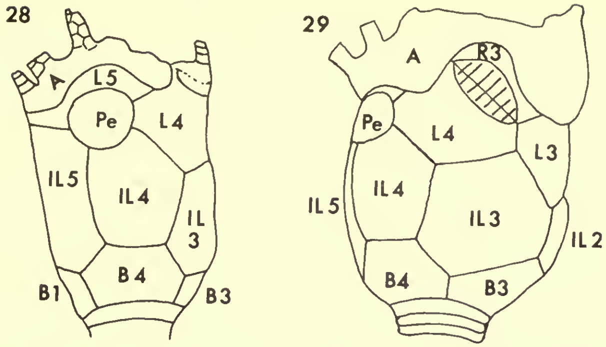


Figs. 26, 27. *Prunocystites fletcheri* Forbes. Fig. 26. Camera lucida drawing of thecal plates visible in holotype. SM. A.10187. Fig. 27. Camera lucida drawing of thecal plates visible in specimen SM. A.10188. A, ambulacrum; BB, basals; ILL, infralaterals; LL, laterals; RR, radials. Note there is no rhomb B2 : IL2.

that the arrangement was the same as in other species of Staurocystinae but a certain amount of variation occurs. The arrangements of the plates visible in three specimens are shown in Text figs. 26–29. The basals unite abapically to form a cicatrix, the ILL and LL circlets are closed but the exact arrangement of the RR and OO is incompletely known. SM. A12579 and DL. 307 show thecal plates ornamented with fine tubercles and larger tubercles at the umbones of the ILL plates. L5 interrupts the RR. circlet in DL. 307.

Two pectinirhombs are present in all but BU. IVa 25 which is quite probably not a specimen of this species. The shape and degree of separation of the half-rhombs vary considerably and are difficult to interpret. BMNH. 40207 shows half-rhomb L4 well and although it is very small it is completely surrounded by a strong raised rim This suggests that the rhomb is fully developed and by inference that the theca was fully grown, although only 5 mm. high. SM. A12579 shows the same rhomb. It is nearly twice as wide (1·7 mm. as opposed to 1·0 mm.) completely conjunct and somewhat angular. This suggests the rhomb was incompletely developed and therefore that the theca was immature. L1 : R5 is distinctly disjunct in BMNH. 40207 but apparently conjunct in the holotype. No rhomb has been seen with more than 7 dichopores in it. In SM. A12579 the slits were 0·07 mm. wide and separated by 0·125 mm. in half-rhomb R3.

The peristomial area is not clearly visible in any specimen but there were definite ambulacra which protruded from the theca. These are best seen in SM. A12579 and DL. 307 where they are confined to the apical region and each ambulacrum has 4 to 6 brachioles. Three ambulacra can be seen and the flooring plates can be distinguished. The brachioles are long and slender, reaching 12 mm. in DL. 307 and tapering from 0·53 mm. wide at the base to 0·47 mm. at the tips. There are at least 44 brachiolars in the most complete brachioles of DL. 307 and the holotype and



FIGS. 28, 29. *Prunocystites fletcheri* Forbes. Fig. 28. Camera lucida drawing of posterior lateral view. Fig. 29. Camera lucida drawing of right lateral view. Note the protruding ambulacra confined to the apex of the theca. A, ambulacrum ; BB, basals ; ILL, infra-laterals ; LL, laterals ; Pe, periproct ; RR, radials. SM. A.12579.

they are individually rather tall and slender. The cover plates of the brachioles are small and pentagonal. There are approximately three to every brachiolar.

The periproct is close to the ambulacra and high up on the theca. This may be a feature of immaturity. In SM. A12579 and DL. 307 the periproct is surrounded by four plates : IL4, IL5, L4 and L5 but in BMNH. 57396 IL4 does not reach the periproct. In the latter specimen there is an anal pyramid of 6 anals and a complete outer circlet of auxiliaries, probably 10 in number. In SM. A12579 the details are not clear but there appears to be only an anal pyramid.

The gonopore and hydropore have not been detected.

The stem is composed of proximal and distal portions. In SM. A10188, which has the most complete stem known, the proximal portion is composed 12 columnals, 6 outer and 6 inner. It is 1·6 mm. long and tapers from 1·25 mm. to 0·6 mm. in this distance. The distal portion is composed of an unknown number of tall thin columnals, tapers from 0·6 mm. to 0·5 mm. and the preserved portion is 28 mm. long. The holotype has 16 proximals, the outer proximals being provided with a smooth external flange aborally. BMNH. 57395, the largest theca that can definitely be assigned to this species, has 20 proximals.

Subfamily **APIOCYSTITINAE** Jaekel 1899

DIAGNOSIS. A subfamily of Callocystitidae with 4 or 5 ambulacra developed in shallow grooves in thecal plates, not strongly protruding.

Genus ***APIOCYSTITES*** Forbes 1848

TYPE SPECIES. *Apiocystites pentrematoides* Forbes 1848.

DIAGNOSIS. A genus of Apiocystitinae with open circlet of radials ; 3 or 4 plates surrounding periproct ; four ambulacra all reaching the column ; three small pectinirhombs.

Both Regnéll (1945 : 92) and Kesling (1963 : 111) state the following :

1. LL and RR circlets closed.
2. Periproct surrounded by three plates (not L4 according to Kesling).
3. Regnéll adds that ILL4 and 5 are not elongated.

Forbes (1848) described this genus and attributed to it the single species *A. pentrematoides* which becomes type species by monotypy. In this species the RR circlet is open, L5 being inserted between R4 and R5, the periproct is surrounded by four plates, namely ILL4 and 5, and LL4 and 5, and finally ILL4 and 5 are elongated in an ad-abapical direction.

The genus *Apiocystites* has been considered to be synonymous with *Lepocrinites* Conrad, 1840 (=*Lepadocrinus* of authors). This latter genus is said to have LL and RR circlets closed and the periproct surrounded by three plates (not L4). It also differs from *Apiocystites* in having ambulacra which do not reach the stem, and in having larger, angular pectinirhombs. In Regnéll's scheme for the Apiocystitinae (1945 : 91) there are only two genera which have an open RR circlet and four plates around the periproct. These are *Tetracystis* Schuchert 1904 and *Jaekelocystis* Schuchert 1903. It is also necessary to compare the present genus with *Lovenicystis* Regnéll 1945, the type species of which has been described as a species of *Apiocystites*.

Tetracystis differs in having protruding ambulacra which are developed on smooth bands on the theca and are characteristic of the Staurocystinae. It also has large angular pectinirhombs with a relatively large number of dichopores. *Jaekelocystis* differs in having specialized pectinirhombs in which one half is reduced to a small pore 0·5 mm. in diameter. *Lovenicystis* differs in having irregular ambulacra which do not reach the stem in all cases, (which do and which do not varies with the individual), in having larger angular rhombs and an incomplete circlet of auxiliaries in the periproct. This latter feature is found rarely in *A. pentrematoides*.

Apparently despite the changes in the diagnosis of the genus *Apiocystites* that have become necessary after re-examination of the type species, it has no junior synonyms and remains a distinct genus. Bassler & Moodey (1943) accepted four species of *Apiocystites* including the type species of *Lovenicystis*. Of the remaining three species it has not been possible to trace a description of *A. anna* Safford and consequently it is impossible to comment on it. *A. elegans* Hall 1851, judging from the figures, is closely related but apparently differs in having three plates around the periproct. This is not a very reliable character (it varies in *Staurocystis quadrifasciatus*) and so the diagnosis has been extended to include this species.

Apiocystites pentrematoides Forbes

(Pl. 5, figs. 8–10 ; Pl. 6, figs. 1–10 ; Pl. 7, fig. 1 ; Pl. 10, figs. 9, 14 ; Text-figs, 30–35)

1848 *Apiocystites pentrematoides* Forbes : 503, pl. 15, figs. 1–9.
1854 *Apiocystites pentrematoides* Forbes ; Murchison : 217, text-fig. 37, fig. 4.
1857 *Apiocystites pentrematoides* Forbes ; Pictet : 298, pl. 99, fig. 14*a–c*.
1867 *Apiocystites pentrematoides* Forbes ; Murchison : 222, text-fig. 55, fig. 4.
1868 *Apiocystites pentrematoides* Forbes ; Bigsby : 24.
1873 *Apiocystites pentrematoides* Forbes ; Salter : 127 (1 fig.).

1876	*Apiocystites pentrematoides* Forbes ; Quenstedt : 680, pl. 113, fig. 80.
1891	*Apiocystis pentremitoides* (sic) (Forbes) Carpenter : 9, 10 (5 figs.), 81.
1899	*Apiocystites pentrematoides* Forbes ; Jaekel : 282, pl. 15, fig. 2.
1904	*Apiocystites pentrematoides* Forbes ; Schuchert : 211.
1943	*Apiocystites pentrematoides* Forbes ; Bassler & Moodey : 52, 130.

DIAGNOSIS. An *Apiocystites* with four plates surrounding periproct.

HOLOTYPE. BMNH. 40187.

MATERIAL. More than 45 specimens in BMNH., BU., GSM., OUM., ?RSM., SM.

HORIZON AND LOCALITY. Wenlock Limestone, Middle Silurian ; Dudley, Worcs.

DESCRIPTION. The theca is ovate elongate and somewhat rounded in cross-section. The mouth, hydropore and gonopore are apical and the anus lateral. The stem was provided with a root structure. The ambulacra are inconspicuous as they are developed in shallow grooves and are flush with the surface of the thecal plates.

The thecal plates are arranged in the usual manner and the arrangement of the first four circlets is as in Text-fig. 30. The arrangement of the orals and adjacent ambulacral flooring plates is shown in Text-fig. 32. There is some variation in the exact position of the ambulacra but little variation in the thecal plating arrangement.

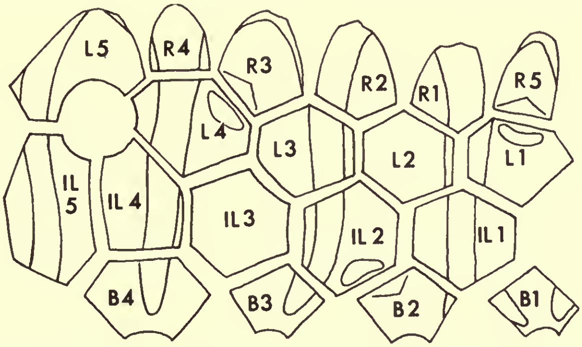


FIG. 30. *Apiocystites pentrematoides* Forbes. Sketch of the arrangement of thecal plates of first four circlets. BB, basals ; ILL, infra-laterals ; LL, laterals ; RR, radials. Based on specimen SM. A.12601.

The basals combine abapically to form a circular cicatrix about 4 mm. in diameter in SM. A12601. Unlike the majority of species of Callocystitidae described the thecal plates are ornamented with fine tubercles and not irregular ridges. This ornamentation is not developed in the shallow curved grooves in which the ambulacra lie. These grooves are smooth and show faint traces of the outlines of the overlying ambulacral flooring plates.

The usual three disjunct pectinirhombs are present. When immature these rhombs tend to be subangular in outline but more often the half-rhombs are distinctly rounded.

B2 : IL2 SM. A12599. This is a compressed rhomb, with distinctly separated halves and measures 3·0 mm. by 2·35 mm. externally. It has 9 dichopores in a

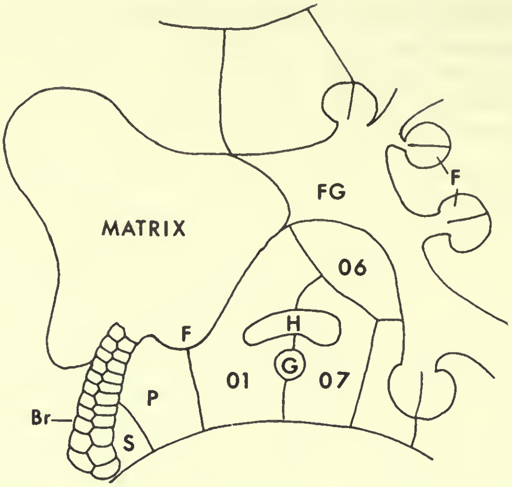


Fig. 31. *Apiocystites pentrematoides* Forbes. Camera lucida drawing of apical region, showing arrangement of food grooves, facets and visible portions of oral plates. Br, brachiole ; F, facet ; FG, food groove ; G, gonopore ; H, hydropore ; OO, orals ; P, primary flooring plate ; S, secondary flooring plate. SM. A.12601.

width of 1·93 mm., the longest reaching 2·47 mm. The slits in B2 are 0·095 mm. wide, separated by 0·10 mm. and reach a length of 0·75 mm. Those in IL2 are obscured by matrix but could not have exceeded 0·5 mm. in length.

L1 : R5 SM. A12601. This is a slightly immature, angular, rhomb and it is depressed. It measures 2·0 mm. by 2·2 mm. externally and has 9 dichopores in a width of 1·9 mm., the longest reaching 1·47 mm. The slits in L1 are 0·14 mm. wide and separated by 0·07 mm. while those in R5 are 0·09 mm. wide and separated by 0·125 mm. The slits in L1 reach a length of 0·47 mm. while those in R5 reach 0·6 mm.

L4 : R3 SM. A12601. This is an equal symmetrical rhomb measuring 2·2 mm. by 2·2 mm. It has 9 dichopores in a width of 1·8 mm., the longest reaching 2·63 mm. The slits in L4 are slightly wider than those in R3 and also shorter.

The mouth was elongate, slightly curved and placed apically at the union of the ambulacra. It was surrounded by the usual 7 orals plates arranged as in Text-fig. 32. The ambulacra are relatively narrow and, in SM. A12601, taper gradually from 1·6 mm. wide apically to about 1·0 mm. at their tips. They broaden considerably apically forming an area 4·2 mm. by 3·3 mm. around the mouth in this specimen. They are developed in shallow grooves and constructed in the same way as other callocystitid ambulacra. They differ from the other species described in having the secondary flooring plates about half the size of the primaries and regularly reaching the ambulacral mid-suture (see Text-fig. 34). The main food groove is relatively narrow and gives off lateral food grooves at a very oblique angle. This adds to the different appearance of this type of ambulacrum (see Text-fig. 33). The flooring plates are apparently unornamented between the lateral food grooves. Both types

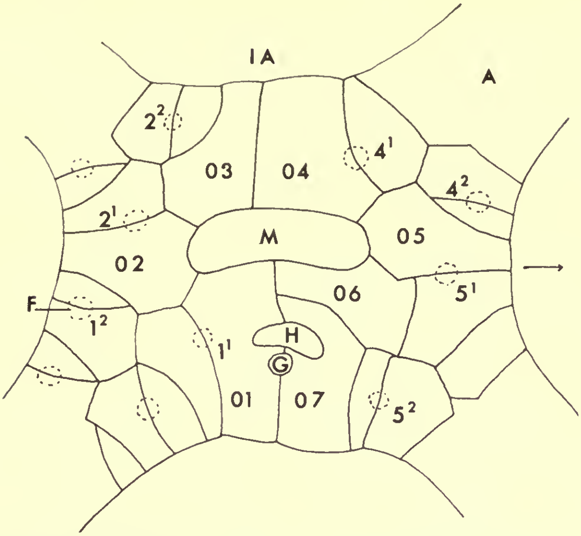
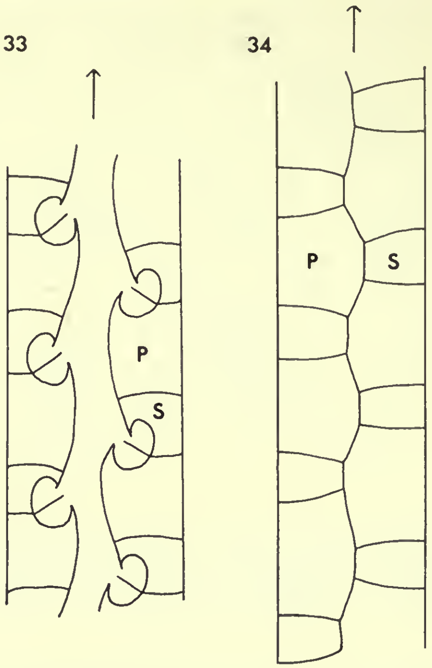


FIG. 32. *Apiocystites pentrematoides* Forbes. Camera lucida drawing of apical region of a weathered specimen, showing arrangement of oral plates and adjacent ambulacral flooring plates. A, ambulacrum; F, position of facets; G, gonopore; H, hydropore; IA, inter-ambulacrum; M, mouth; OO, orals. The arrow points to the periproct. BU., unregistered.

of food groove are provided with small cover plates which are also unornamented. The brachiole facets are small circular pits in the flooring plates. The brachioles are slender and relatively widely spaced. This last feature varies considerably. The average of ten measurements was 4 brachioles in 4·72 mm. but varied from 4 in 3·73 mm. to 4 in 5·6 mm. The brachioles may reach 2·7 mm. in length and are only 0·3 mm. wide at the base. They are composed of approximately 30 brachiolars.

The periproct is surrounded by four plates which are: ILL4 and 5 and LL4 and 5. L5 contributes approximately a third of the border, and the other three contributing about equally to the remaining two-thirds. There is no periproct hood in L5. The periproct is almost level with the general surface of the theca and 1·6 mm. in diameter in SM. A12601. Within the narrow but complete circlet of auxiliaries in this specimen there is a slightly elevated anal pyramid 1·3 mm. in diameter and composed of 6 anals. In some examples the auxiliary circlet may be incomplete. This is the case in BMNH. 57392 where there are only 5 auxiliaries abapically. In the complete circlet of BMNH. 40188 there are only 6 auxiliaries and 7 in BMNH. 25533 and E.29074. Both the anals and auxiliaries are unornamented.

The gonopore and hydropore are apical and shared by O1 and O7. The hydropore is semicircular and somewhat slit-like and is adapical to the gonopore. In BMNH. 40153 the gonopore is covered by a pyramid of 4 gonals (see Text-fig. 35). The hydropore and gonopore may be quite separate as in SM. A12601 (Text-fig. 31) or the hydropore may be wrapped around the gonopore as in BMNH. 40153 (Text-fig. 35).



Figs. 33, 34. *Apiocystites pentrematoides* Forbes. Fig. 33. Sketch of part of an ambulacrum. Based on specimen SM. A.12599. Fig. 34. Sketch of impression of ambulacral flooring plates on the thecal plates. P, primary flooring plate ; S, secondary flooring plate. The arrows point to the mouth. Based on specimen SM. A.12597.

The stem is typical of the Callocystitidae but from what is known the distal portion is reduced, and may merge gradually into the proximal portion. SM. A12599 has a complete stem terminating in a root structure (see Pl. 10, fig. 14). It is 20 mm. long compared with a thecal height of 15 mm. The proximal portion is relatively large,

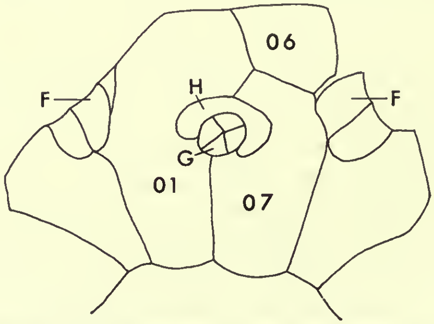


Fig. 35. *Apiocystites pentrematoides* Forbes. Sketch of the area around the gonopore and hydropore, showing gonopore closed by pyramid of four gonals and closely approximated to hydropore. F, facet ; G, gonopore ; H, hydropore ; OO, orals. Cf. Text-fig. 31. Based on specimen BMNH. 40153.

at least 13 mm. long, and tapers from 4·5 mm. at the base of the theca to about 2·5 mm. The distal portion is very short and narrow. In BMNH. 48192 the stem is shorter than the thecal height and the distal portion consists of only 5 columnals. There are 8 outer proximals in this specimen and 17 or 18 in SM. A12601. The outer columnals are provided with an external flange which is slightly beaded with fine tubercles in well preserved examples.

Family **ECHINOENCRINITIDAE** Bather 1899

Diagnosis. A family of Glyptocystitida with typically produced periproct composed of anal pyramid and single circlet of auxiliaries ; with short ambulacra restricted to apex of theca. Modified from Kesling (1963).

Within this family the rhombs are all disjunct pectinirhombs, but there are two different types. In *Echinoencrinites*, and the other Ordovician genera except *Scoliocystis*, all the dichopores of each rhomb are discrete entities and they open externally in slits which are level with the surface of the thecal plates. The slits are isolated from each other and provided individually with very narrow raised rims. In the Silurian genera, and *Scoliocystis*, the walls of individual dichopores in a rhomb are continuous with those of the adjacent dichopores at the external surface and the dichopores are effectively folds in the thecal plates. All the slits of one half-rhomb open in a depression or *vestibule* which is provided, as a whole, with a raised rim. This rim is open in one half-rhomb and closed in the other. The *Echinoencrinites* type of disjunct pectinirhomb was common in the Ordovician but the other type predominates in the Silurian and Devonian. The latter type was more efficient and was independently acquired by several families of Glyptocystitida. If Jaekel's figures of *Scoliocystis* (Jaekel 1899, pl. 11, figs. 10, 10*a*, 11) are accurate then it must be the ancestor of the British Silurian echinoencrinitids, and these three genera may be distinguished from the others by their advanced type of pectinirhomb. Jaekel (1899) proposed the family Scoliocystidae which was unfortunately pre-occupied by Bather's Echinoencrinitidae published earlier in the same year. The name is now resurrected for a subfamily of the Echinoencrinitidae containing the genus *Scoliocystis*. The Echinoencrinitidae may therefore be divided into the following two subfamilies :

Subfamily **ECHINOENCRINITINAE** nov.

Diagnosis. A subfamily of Echinoencrinitidae with disjunct pectinirhombs composed of dichopores opening as discrete slits, individually surrounded by slight rims and level with external surface of thecal plates.

Subfamily **SCOLIOCYSTINAE** Jaekel 1899 emend

Diagnosis. A subfamily of Echinoencrinitidae with disjunct pectinirhombs composed of dichopores opening as slits within vestibules, collectively surrounded by a rim.

Genus *GLANSICYSTIS* nov.

As stated earlier the removal of *Prunocystites fletcheri* from the Echinoencrinitidae to the Staurocystinae necessitates the description of a new genus for "*Echinoencrinites*" *baccatus* Forbes.

DIAGNOSIS. A genus of Scoliocystinae with ovate theca, four plates surrounding periproct, L5 interrupting the RR circlet, three pectinirhombs.

TYPE SPECIES. *Echinoencrinites baccatus* Forbes 1848.

Glansicystis baccata (Forbes)

(Pl. 7, figs. 2–18 ; Pl. 8, figs. 1–3 ; Pl. 10, figs. 10, 11 ; Text-figs. 36–39)

1848 *Echinoencrinites baccatus* Forbes : 506, pl. 17, figs. 1–11.
1854 *Echinoencrinites baccatus* Forbes ; Murchison : 217, text-fig. 37, fig. 5.
1857 *Echinoencrinites baccatus* Forbes ; Pictet : 300.
1867 *Echinoencrinites baccatus* Forbes ; Murchison : 222, text-fig. 55, fig. 5.
1868 *Echinoencrinites baccatus* Forbes ; Bigsby : 25.
1873 *Echinoencrinites baccatus* Forbes ; Salter : 128.
1876 *Echinoencrinus baccatus* (Forbes) Quenstedt : 676, pl. 113, fig. 70. (3 figs.).
1896*a* *Echinocystis baccata* (Forbes) Haeckel : 146.
1899 *Prunocystites baccatus* (Forbes) Jaekel : 263.
1900 *Prunocystites baccatus* (Forbes) ; Bather : 60.
1943 *Prunocystites baccatus* (Forbes) ; Bassler & Moodey : 53, 184.

DIAGNOSIS. As for the genus.

LECTOTYPE. GSM. 7380. The original specimen of Forbes (1848, pl. 17, figs. 1, 3, 4).

MATERIAL. About 30 specimens of which three (BMNH. E.29057 ; GSM. 7380, 103101) are of the typical form. These are in BMNH., BU., GSM., OUM., SM.

HORIZON AND LOCALITY. Wenlock Limestone, Middle Silurian ; Dudley, Worcs. and Walsall, Staffs.

DESCRIPTION. The theca is elongate ovate with brachioles developed apically around the mouth. The anus is lateral and just over half way up the theca while the

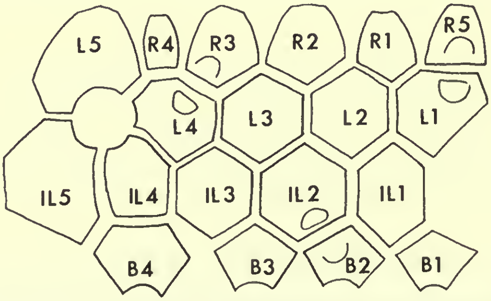


FIG. 36. *Glansicystis baccata* (Forbes). Sketch of arrangement of thecal plates of first four circlets. BB, basals ; ILL, infra-laterals ; LL, laterals ; RR, radials. Based on specimen SM. A.12578.

gonopore and hydropore are apical. Three disjunct pectinirhombs and the usual type of stem are present.

The thecal plates are arranged in definite circlets and the usual formula may be given. The typical plating arrangement of the first four circlets is shown in Text-fig. 36. There is considerable variation however. Text-fig. 37 shows an arrangement in which ILL1–4 form a closed circlet and Text-fig. 38 another unusual arrangement in which there are 6 RR and L5 does not interrupt the RR circlet. Both these specimens appear to be anomolous. The four basals combine abapically to form a circular cicatrix 4 mm. in diameter in SM. A12577. There were 7 orals, 6 of which reach the peristome and contribute to its margin, as in the other Glyptocystitida. The odd oral is O7 (Text-fig. 39). The size of the area occupied by the orals varies and is associated with two distinct trends within this species. In the lectotype and two other specimens (GSM. 103101, BMNH. E.29057) the area occupied by the orals is small (Pl. 7, fig. 8) while in the other examples this area is larger (Pl. 7, fig. 2). The plates of the type and the two examples mentioned above are ornamented with ramifying irregular raised pustules while those of all other specimens are ornamented with fine granules. There is also a tendency for the plates of the typical form to be much more tumid and the sutures deeper than in the other form.

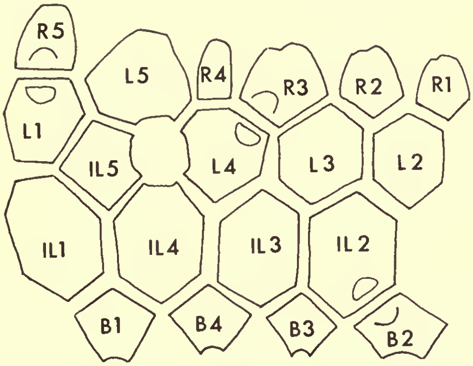


FIG. 37. *Glansicystis baccata* (Forbes). Sketch of unusual arrangement of thecal plates in which IL5 has been elevated in the theca allowing ILL1–4 to form a closed circlet. BB, basals; ILL, infra-laterals; LL, laterals; RR, radials. SM. A.12577.

There are three disjunct pectinirhombs with half-rhombs with semi-circular outlines. All have few dichopores and prominent rims which are closed on IL2, L1 and L4. These rims are more strongly developed on the typical form than on the others.

B2 : IL2 BMNH. E.29057. This is a compressed rhomb measuring 2·8 mm. by 2·3 mm. with 8 dichopores in a width of 1·73 mm., the longest reaching 2·23 mm. The slits in both B2 and IL2 are 0·09 mm. wide and separated by 0·125 mm. In both half-rhombs they reach a maximum length of 0·65 mm.

L1 : R5 (Lectotype). This is a compressed rhomb measuring 3·53 mm. by 2·8 mm. externally with 8 dichopores in a width of 1·73 mm. The extra millimetre in the width is entirely taken up by the prominent rhomb rim in L1. The longest dichopore is approximately 1·75 mm. long. The slits in L1 are 0·107 mm. wide and separated by 0·125 mm. while those in R5 are only 0·07 mm. wide and separated by 0·14 mm. The slits in L1 reach a maximum length of 0·6 mm. and those of R5 marginally longer. The same rhomb in SM. A12577 is highly compressed, being twice as long as wide, has 7 dichopores and a much less conspicuous rim on L1.

L4 : R3 (BMNH. E.29057). This is a compressed rhomb measuring 4·33 mm. by 3·05 mm. with 10 dichopores in a width of 2·47 mm., the longest reaching 3·0 mm. The slits on L4 are obscured by matrix but those on R3 are 0·07 mm. wide and separated by 0·14 mm. They reach a length of approximately 0·75 mm. The same rhomb in SM. A12577 has only 8 dichopores, a much less conspicuous rim on L4, and is again more distinctly compressed.

The ambulacra in the typical form are restricted to the oral plates and give rise to two large, and possibly two small, facets in the lectotype. In the other form the ambulacra may extend on to radial plates (Pl. 7, fig. 2) and have up to 3 facets in one ambulacrum. The maximum number of facets seen was 7. There may well be four ambulacra of which 1 and 4 terminate in a single large facet (the first formed) while ambulacra 2 and 5 may add up to three facets. This interpretation is not certain. The orals are ornamented between the ambulacra in the same way as the other thecal plates. The food grooves are broad and deep and covered by alternating cover plates which are unornamented. Apparently the cover plates were unable to articulate with the orals or flooring plates and were lodged in grooves in these plates. These grooves enlarged as the ambulacra grew. The mouth is a more or less central, oval opening. The facets are set in quite deep depressions in the oral or flooring plates. The brachioles are preserved in BU. H063 where they are at least 12 mm. long (none appears to be complete) and are composed of at least 50 brachiolars. As far as can be determined they do not taper in the preserved portion and are 0·75 mm. wide. The food groove was provided with cover plates and these are 2 to 3 times as numerous as the brachiolars.

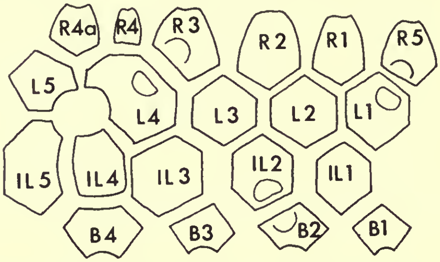


FIG. 38. *Glansicystis baccata* (Forbes). Sketch of unusual arrangement of thecal plates in which there are six radial plates forming a closed circlet. BB, basals ; ILL, infralaterals ; LL, laterals ; RR, radials. BMNH. E.29057.

The periproct is surrounded by four plates which are : ILL4 and 5 and LL4 and 5. Apart from the two anomolous specimens figured in Text-figs. 37 and 38 the arrangement is constant. L5 contributes just less than a third of the border and the other three plates share more or less equally in the remaining two-thirds. In the typical form there appear to be 12 auxiliaries forming a complete circlet but only half this number are found in SM. A12577 and possibly 7 in SM. A12578, still forming a complete circlet. The anal pyramid is composed of 6 anals in SM. A12577, the only specimen in which the number can be made out. The ornament of the auxiliaries, and probably the anals as well, is the same as that of the thecal plates and consequently this is more marked in the typical form.

The gonopore and hydropore are set apically across the common suture of OO1 and 7. The hydropore is elongate, slightly curved and adoral. The gonopore is circular and covered by a gonal pyramid of an unknown number of gonals. In both forms of the species both apertures are set in a diamond shaped depression in OO1 and 7.

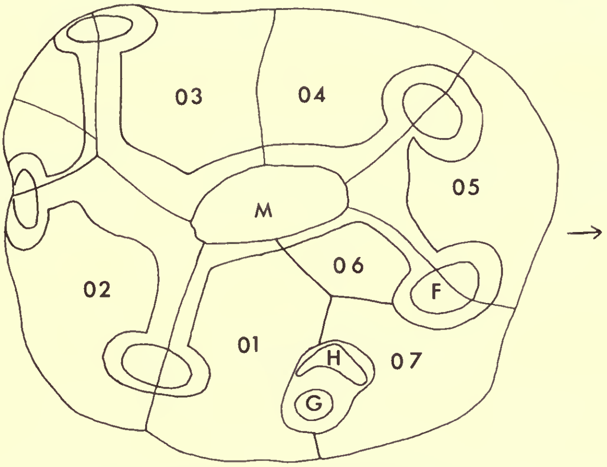


Fig. 39. *Glansicystis baccata* (Forbes). Camera lucida drawing of apical region. F, facet ; G, gonopore ; H, hydropore ; M, mouth ; OO, orals. The arrow points to the periproct. Based on specimen OUM. C.518.

The stem is composed of a proximal and a distal portion as in all other Glyptocystitida. A complete stem is preserved in BU. H025. The stem is 12–13 mm. long compared with a thecal height of 10 mm. The proximal portion has 12 outer columnals tapering from just under 3 mm. to half that, in a distance of about 6 mm. The outer proximals are provided with an external flange that may have one or two rings of fine tubercles developed on it. The distal portion is composed of 18 distinct columnals and a few more fused into the root structure. The proximal 8 are in distinct pairs, thereafter the columnals are exceptionally thin. The stem is attached to a polyzoan.

REMARKS. There are two distinct forms of this species, the typical form of the lectotype, and the common form. The possibility that these represent two distinct species cannot be ruled out. Unfortunately there are only three specimens of the typical form which is too small a number to give an accurate impression of the variation. Even so, one of these specimens has an aberrant plating arrangement (BMNH.

E.29057). The main points of difference are the thecal ornamentation, the area of the orals, the degree of impression of the sutures and consequently the tumidity of the plates, and the strength of the development of the rhomb rims. Thecal ornamentation is very variable in the next species, *Schizocystis armata*, where two analogous variations occur and it does not correlate with any other features. This character would seem to be an unreliable one taxonomically. Some specimens of the common form have tumid plates and relatively deep sutures like the typical form. This leaves only the size of the oral area and the strongly developed rhomb rims. Again in the next species the rhomb rims show considerable variation which is not correlated with any other feature so this too may be unreliable. In view of the wide variation shown by the common form it is thought wise to regard the typical form as merely another variation, albeit more distinct, especially as there are so few specimens on which to base an impression of its variability.

Genus ***SCHIZOCYSTIS*** Jaekel 1895

DIAGNOSIS. A genus of Scoliocystinae with theca ovate aborally and laterally compressed adorally; brachioles on two short ambulacra running anteriorly and posteriorly across top of theca; strongly protruding periproct surrounded by four plates.

TYPE SPECIES. *Echinoencrinites armatus* Forbes 1848.

Schizocystis armata (Forbes)

(Pl. 8, figs. 5–11; Pl. 9, figs. 1–9; Pl. 10, figs. 15, 16; Text-figs. 40–44)

1848 *Echinoencrinites armatus* Forbes : 507, pl. 18, figs. 1–14, pl. 19, figs. 1–10.
1854 *Echinoencrinites armatus* Forbes; Murchison : 217, text-fig. 37, fig. 6 (3 figs.).
1857 *Echinoencrinites armatus* Forbes; Pictet : 300, pl. 99, fig. 17 (3 figs.).
1865 *Echinoencrinus armatus* (Forbes) Rofe : 251, pl. 8, figs. 10, 11.
1867 *Echinoencrinites armatus* Forbes; Murchison : 222, text-fig. 55, fig. 6 (3 figs.).
1868 *Echinoencrinites arenatus* (sic) Forbes; Bigsby : 25.
1873 *Echinoencrinites armatus* Forbes; Salter : 127 (fig.), 128.
1875 *Echinoencrinus armatus* (Forbes); Bailey : 54, pl. 18, fig. 7.
1876 *Echinoencrinus armatus* (Forbes); Quenstedt : 675, pl. 113, figs. 68 (5 figs.), 69.
1891 *Echinoencrinus armatus* (Forbes); Woods : 43.
1891 *Echinoencrinus armatus* (Forbes); Carpenter : 7, pl. 1, fig. 3.
1895 *Schizocystis armatus* (Forbes) Jaekel : 113.
1896*a* *Echinocystis armata* (Forbes) Haeckel : 140, pl. 4, figs. 31–34.
1899 *Schizocystis armata* (Forbes); Jaekel : 266, pl. 12, figs. 1, 1*a–c*, 2.
1900 *Schizocystis armata* (Forbes); Bather : 61, text-figs. 25–27.
1943 *Schizocystis armata* (Forbes); Bassler & Moodey : 53, 188.
1945 *Schizocystis armata* (Forbes); Delpey : 261, text-fig. 8.
1953 *Schizocystis armata* (Forbes); Cuénot : 261, text-fig. 19.

DIAGNOSIS. As for the genus.

LECTOTYPE. GSM. 7381 is the original of Forbes (1848, pl. 18, figs. 1–4), and although it is incomplete it is the most suitable specimen here selected as lectotype.

Material About 125 specimens in BMNH., BU., GSM., OUM., RSM., SM. Of these 45 have 2 rhombs, 15 have 3 and 30 are indeterminate. Information is not available for the remainder.

Horizon and locality. Wenlock Shale, Middle Silurian; Dudley, Walsall, Hurst Hill, Malvern, May Hill, Pen-y-lan.

Description. The theca is sac-like, laterally compressed adorally and tumid aborally. The left side is concave or flat adorally and convex aborally, while the right side is gently convex throughout. The mouth was at the confluence of the two short ambulacra which run anteriorly and posteriorly along the crest of the theca. The posterior is the shorter. The gonopore and hydropore are apical on the left side of the theca and the anus is lateral, about half way up the theca. The anus, half-rhomb rims and the umbones of the ILL plates all protrude strongly giving the theca a tubercular appearance. The stem was aboral and lacked a root structure.

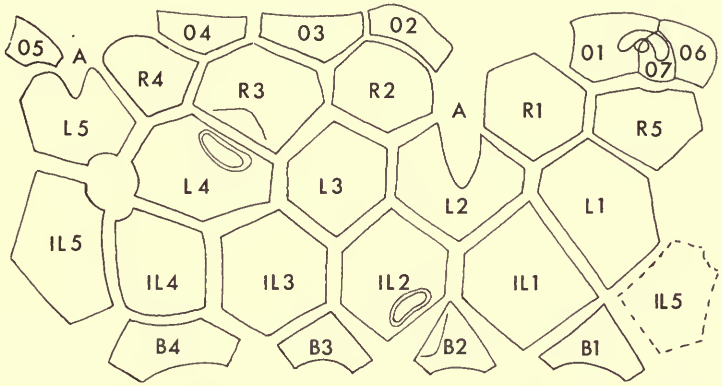


Fig. 40. *Schizocystis armata* (Forbes). AA, ambulacra; BB, basals; ILL, infra-laterals; LL, laterals; OO, orals; RR, radials. Based on specimen SM. A.12592.

The arrangement of the thecal plates is shown in Text-fig. 40, but there is a certain amount of variation in the details. In the specimen illustrated in Text-fig. 40 the ILL only just form a closed circlet, IL1 and IL5 meeting at a point. In several other thecae all the ILL have long common sutures. In SM A10197 (Text-fig. 41) L4 and L3 only just meet at a point and L1 is an unusual shape. Presumably all these variations were related to variability in the total shape and size of the thecae in this species. The lengths of the ambulacra also vary considerably. In SM. A10197 both just reach the lateral plates forming slight embayments in the margins of L2 and L5. In other specimens the ambulacra extend well on to these plates and the posterior may reach the edge of the periproct. This feature is not related to size apparently. The basals have very short common sutures and the pentagonal ones are very sharply pointed. They unite abapically forming a circular cicatrix 5·5 mm. in diameter in SM. A10197. The orals are strung out along the sides of the ambulacra in an unusual arrangement. OO2, 3 and 4 are on the right side of the theca (Text-fig. 42) and OO5, 6, 7 and 1 on the left (Text-fig. 43). The remainder of the ambulacra are composed of flooring plates.

The ornamentation of the thecal plates is very variable (see Pl. 8, figs. 5, 6 ; Pl. 9, figs. 3, 5). In SM. A12592 it is of irregular tubercles and rounded ridges, giving the thecal surface an uneven appearance, and the umbones of the ILL plates are not very strongly developed. In the lectotype the plates are finely granulated and the umbones of the ILL plates are very prominent. This ornament is very common and typical. The strength and density of the granulations varies from plates which appear almost smooth to plates that appear to be prickly. In extreme cases some of the tubercles unite to form strong intermittent radiating ridges as in the specimen figured on Pl. 9, fig. 3.

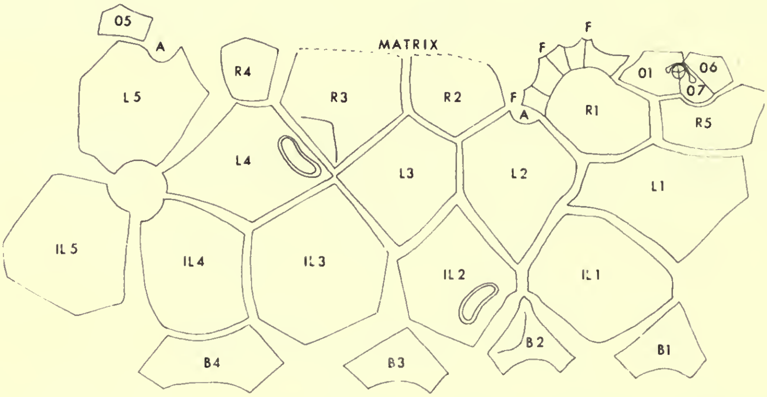


FIG. 41. *Schizocystis armata* (Forbes). Sketch of arrangement of thecal plates. AA, ambulacra ; BB, basals ; F, facet ; ILL, infra-laterals ; LL, laterals ; OO, orals ; RR, radials. SM. A.10197.

There may be two or three rhombs present and the two and three-rhombed forms differ in the details of the gonopore and hydropore, and the adoral portions of the two ambulacra. B2 : IL2 and L4 : R3 are always present but L1 : R5 may or may not be developed. Apparently the three-rhombed form is commoner at Malvern than at Dudley or Walsall but apart from this there is little difference in distribution. At all three localities the two-rhombed form is commoner than the three-rhombed.

B2 : IL2 (SM. A12592). This rhomb is compressed and measures 4·35 mm. by 4·0 mm. externally. It has 15 dichopores. The slits in B2 reach a length of 1·1 mm. They are 0·07 mm. wide and separated by 0·125 mm. The slits of IL2 are obscured by matrix but could not have reached the same length as those in B2.

L4 : R3 (SM. A12592). This rhomb is also compressed and measures 4·5 mm. by 4·0 mm. It has 15 dichopores whose slits reach a length of 1·16 mm. in R3 but only 0·7 mm. in L4. The slits in L4 are slightly wider than those in R3.

SM. A12583 has all three rhombs. B2 : IL2 has 17 dichopores ; L4 : R3 has 12, and L1 : R5 has 10.

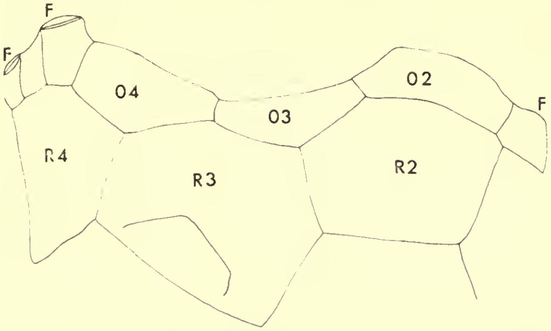


FIG. 42. *Schizocystis armata* (Forbes). Camera lucida drawing of adapical region of right side. F, facet; OO, orals; RR, radials. SM. A.12592.

The mouth has not been directly observed but lay apically at the confluence of the two ambulacra. The anterior ambulacrum was the longer and has three facets to the left in SM. A10197; the posterior having only 2. In SM. A12592 the anterior had 5 smaller facets, 4 to the left and 1 to the right, while the posterior had three facets all to the left of the ambulacrum. Both ambulacra are longer in the latter example although it has a smaller theca. Although there is considerable variation in the length and number of facets the majority of the facets is always to the left of the ambulacrum. Thus the food grooves of the brachioles of the posterior ambulacrum may be inferred to have faced the left of the theca and those in the anterior, the right of the theca.

Near the mouth the oral plates contribute to the ambulacra and these give way distally to the ambulacral flooring plates. There are no facets developed on the oral plates and each facet is formed of two ambulacral flooring plates as in all other Glyptocystitida. In the two-rhombed forms the adoral portion of the food groove forms a gentle curve, concave to the left side of the theca. OO6, 7 and 1 are bent over to fill this concavity and consequently they face directly upwards (see Pl. 9, fig. 1). The gonopore and hydropore also face in this direction. In the three-rhombed forms the adoral portion of the food groove forms an S-shaped curve with the portion above the gonopore and hydropore convex to the left of the theca. OO6, 7 and 1 face to the left of the theca in this form and so do the gonopore and hydropore (see Pl. 9, fig. 7). The food groove was covered with flooring plates which were ornamented with fine pustules. They are relatively large plates and alternate regularly. The lateral food grooves are short and very oblique. Brachioles are preserved on OUM. C.398 and are long and slender. They taper evenly right up to the tip and were composed of about 100 brachiolars. There is no evidence of twisting of the food groove and the brachioles may reach twice the length of the theca.

The periproct was surrounded by four plates which are ILL4 and 5, and LL4 and 5. There is a strongly protruding anal pyramid composed of five anals and surrounded by a complete set of 10 auxiliaries in SM. A10197. The auxiliaries are frequently more strongly developed adorally and to the right than at other points around the periproct and this causes the anal pyramid to point to the left and aborally. This is not univer-

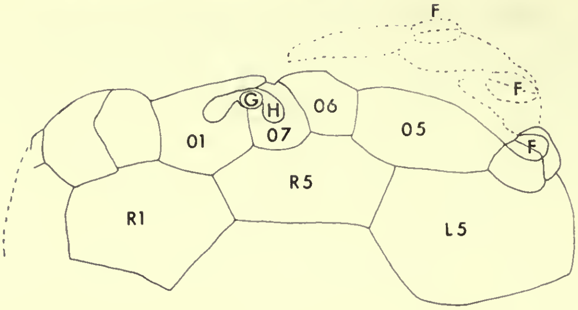


FIG. 43. *Schizocystis armata* (Forbes). Camera lucida drawing of adapical portion of left side. F, facet; G, gonopore; H, hydropore; OO, orals; RR, radials. SM. A.12592.

sal however. In SM. A10197 the periproct is 2 mm. in diameter and, although incomplete, protrudes 1·2 mm. from the level of the theca.

The gonopore and hydropore lay apically across the common suture of OO1 and 7. The hydropore was curved, bilobed and the adoral of the pair. It was provided with a rim. The gonopore is small, circular and covered with a pyramid of 3 or 4 gonals. In SM. A10197 it is 0·5 mm. in diameter. As previously stated the direction in which these orifices face depends on whether there are two or three rhombs developed.

The stem was typical of the Glyptocystitida being divisible into proximal and distal portions. On SM. A12585 the outer proximals are smooth and ring-like but have an aboral ring of fine tubercles. One GSM. specimen has slightly compressed proximals with a slight crest developed posteriorly but this could be aberrant. In OUM. C398 the distal columnals are smooth and differ from the proximals in being taller and thinner. The stem gradually tapers throughout its length. BMNH. 57442 has a virtually complete stem. It is about 32 mm. long and tapers from 4 mm. at the base of the theca to approximately 0·5 mm. at the tip. The proximal portion has 11 outer proximals provided with a ring of fine tubercles aborally. There are 26 to 28 distals which alternate regularly, the larger being provided with a central ring of tubercles developed on a distinct flange. The distal portion tapers regularly to a point.

SM. A8137*a* is an internal mould of a specimen from the May Hill inlier. It is preserved in a light brown material and clearly shows the plate margins etc. Developed somewhat irregularly over the surface is a reticular pattern of dark brown lines. These lines are composed of a different material to the rest of the internal mould and appear to be just too regular to be preservational in origin yet not quite regular enough to be certain they are organic in origin. The pattern is indicated in Text-fig. 44 and the lines appear to form a ring in the centres of the plates and to give off one, or rarely two, trans-sutural branches which join up with the central ring of the neighbouring plates. The significance of this pattern is not understood. The associated specimen from the same piece of rock does not show this feature on its internal mould (Pl. 9, fig. 8).

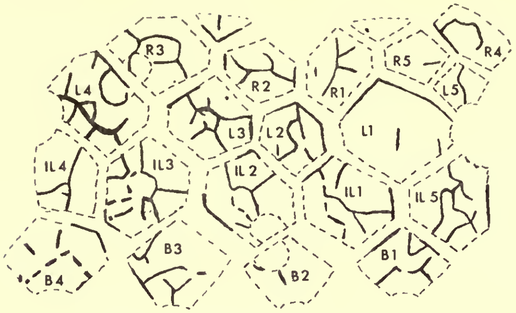


FIG. 44. *Schizocystis armata* (Forbes). Sketch of thecal plates of internal mould, showing reticular structure described in text. The specimen is unusual in having 5 plates surrounding the periproct, but as it is an internal mould direct comparisons with external views cannot be made. SM. A.8137*a*.

REMARKS. As with the preceding species there are two fairly distinct forms of this species, which may be referred to as the two- and three-rhombed forms. These two forms are thought to have had slightly different modes of life but this cannot of course be confirmed. There is considerable difficulty in envisaging a mode of life which explains satisfactorily all the morphological adaptations of this species let alone imagining two for a pair of ecological subspecies which these two forms may well represent. As with the last species it is thought wiser to refer all the specimens to a single species while recognizing that two more or less distinct forms occur. It is not thought that these two forms could represent sexual dimorphism in *Schizocystis* as there is no significant difference in the gonopore of the two forms, which might be expected in that case.

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PLATE 1

Stereophotos of ***Staurocystis quadrifasciatus*** (Pearce)

FIG. 1. Apical view showing area occupied by oral plates.

FIG. 2. Abapical view showing ambulacra nearly reaching the circular cicatrix with wide lumen, and damaged rhomb B2 : IL2.

FIG. 3. Posterior lateral view.

FIG. 4. Anterior lateral view, showing plate ornamentation.

FIG. 5. Right lateral view.

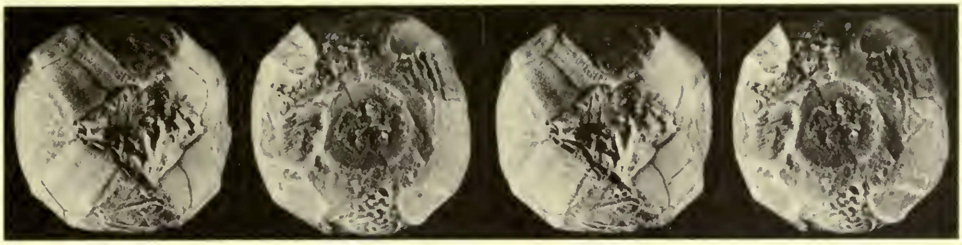
FIG. 6. Left lateral view, showing impressions of ambulacral flooring plates on the thecal plates in the ambulacrum to the right (amb. 5).

FIG. 7. Posterior lateral view showing details of periproct. Note periproct surrounded by three thecal plates and the hood formed in adapical plate (L5). The circlet of auxiliaries is closed but the adapical plates are very much reduced and do not show clearly.

FIG. 8. Left lateral view showing details of brachioles. The coiled brachiole is complete and composed of 37 or 38 brachiolars.

All ×2. All specimens whitened with ammonium chloride sublimate.

Figs. 1–6 (SM. A.28230) ; Fig. 7 (BU. H041) ; Fig. 8 (BU. H018).



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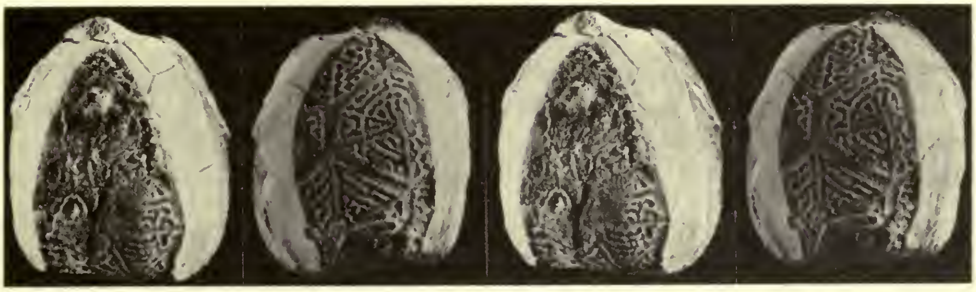

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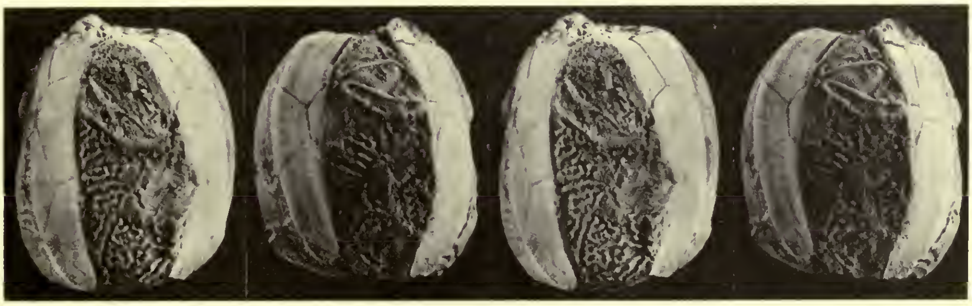

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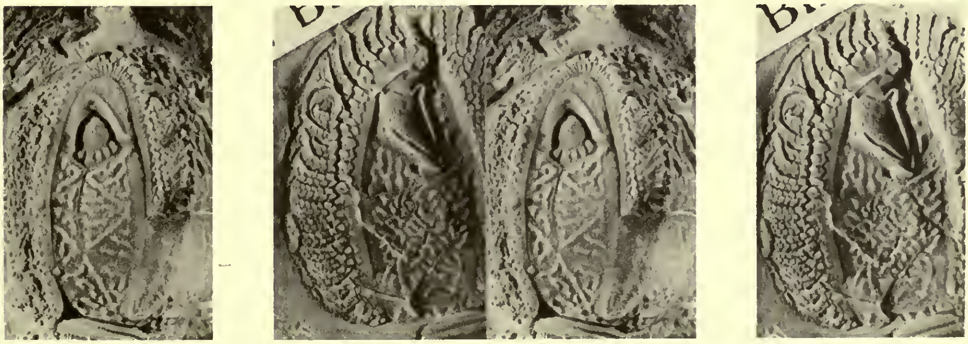

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PLATE 2

Stereophotos of
Staurocystis quadrifasciatus (Pearce) and ***Pseudocrinites bifasciatus*** (Pearce)

Staurocystis quadrifasciatus (Pearce)

FIG. 1. Apical view showing details of the ambulacra around the mouth (cf. Text-figs. 4, 9).

FIG. 2. Aberrant specimen showing growth of rhomb L4 : R3 partly inhibited by proximity of ambulacrum 4.

FIG. 3. Posterior lateral view showing details of ambulacra and periproct. There are four plates surrounding the periproct and the hood is ornamented. In the ambulacra the brachioles touch basally and there is a single tubercle between adjacent lateral food grooves not shown in Text-fig. 11.

Pseudocrinites bifasciatus Pearce

FIG. 4. Lateral view of ambulacrum 2 showing impressions of ambulacral flooring plates on the thecal plates.

Fig. 5. Apical view.

FIG. 6. Lateral view of periproctal face showing partly preserved anal pyramid and auxiliary circlet, rhomb L4 : R3, and plate ornamentation.

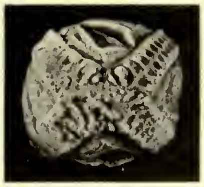
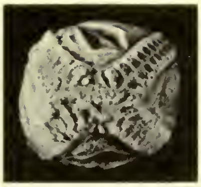
FIG. 7. Lateral view of gonal face showing well preserved rhomb B2 : IL2.

FIG. 8. Abapical view showing the ambulacra reaching the cicatrix.

All ×2. All specimens whitened with ammonium chloride sublimate.

Fig. 1 (BU. H042) ; Fig. 2 (BMNH. 57385) ; Fig. 3 (BMNH. E.7555) ; Figs. 4–8 (SM. A. 12593).

PLATE 2

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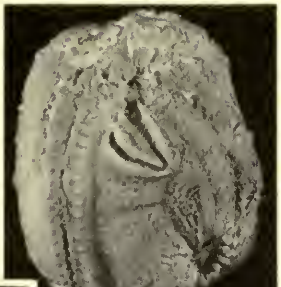
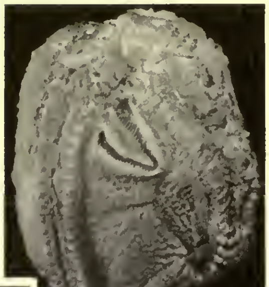

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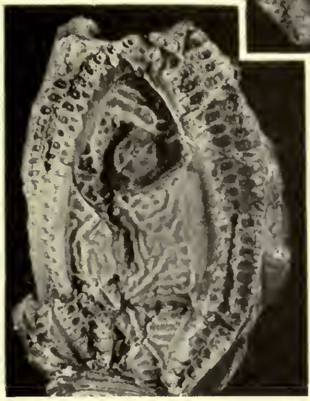
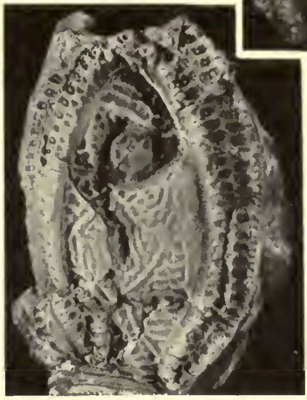

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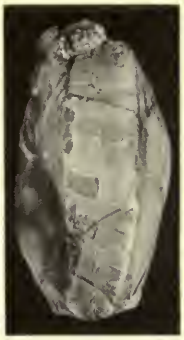
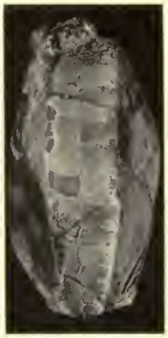

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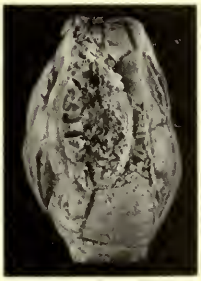
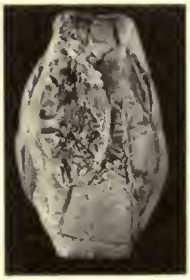

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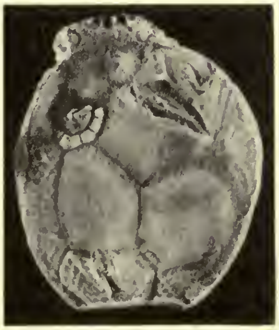
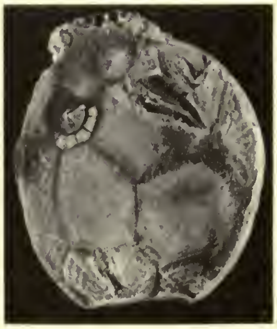

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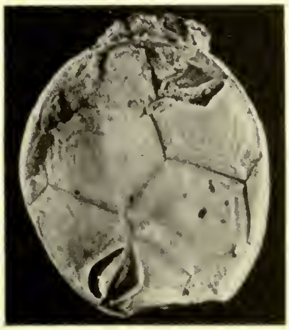
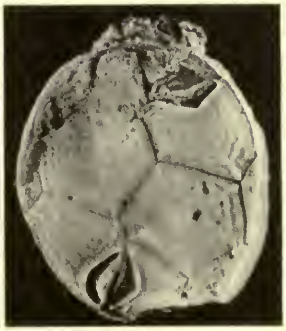

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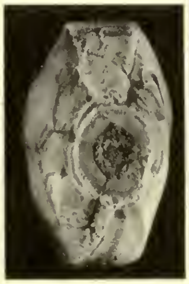
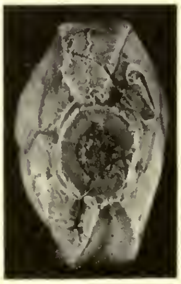

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PLATE 3

Stereophotos of *Pseudocrinites bifasciatus* Pearce, *P. pyriformis* sp. n. and *Prunocystites fletcheri* Forbes

Pseudocrinites pyriformis sp. n.

FIG. 1. Lateral view of gonal face showing the ornamentation of ad- and abapical thecal plates and ambulacral flooring plates, and well preserved rhomb L1 : R5. Holotype, BU. H010.

FIG. 7. Lateral view of periproctal face of same specimen.

Pseudocrinites bifasciatus Pearce

FIG. 2. Lateral view of periproctal face showing initial plate ornamentation. BU. H012.

FIG. 3. Same, lateral view of ambulacrum 2 which nearly reaches the cicatrix even at this early growth stage. Note rhomb B2 : IL2 is conjunct.

FIG. 4. Same, apical view.

FIG. 5. Apical view showing area occupied by oral plates. BMNH. 40192.

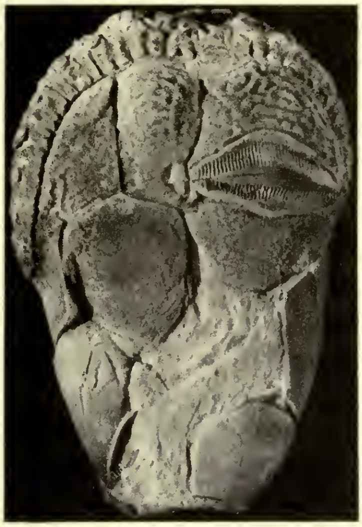
FIG. 6. Apical view showing visible portions of oral plates. SM. A.10192.

Prunocystites fletcheri Forbes

FIG. 8. Lateral view showing growth lines on thecal plates. Note the well formed rim on the rhomb to the left. BMNH. 40207.

FIG. 9. Lateral view showing ambulacra and conjunct rhomb. SM. A.12579.

Fig. 6 ×5. All others ×2. All specimens whitened with ammonium chloride sublimate.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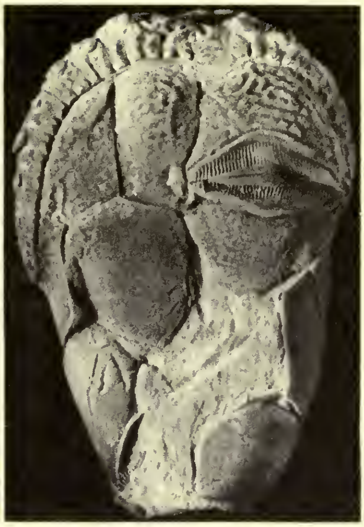

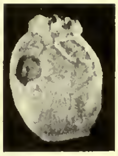
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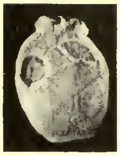

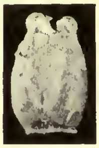
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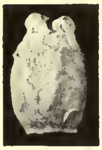

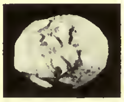
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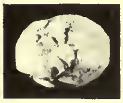

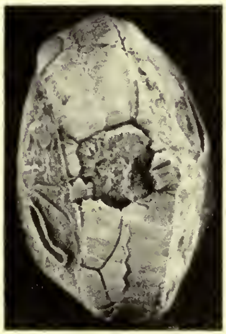
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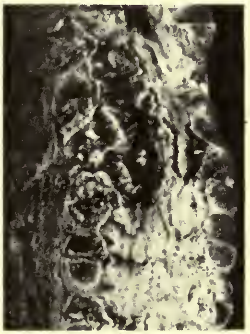
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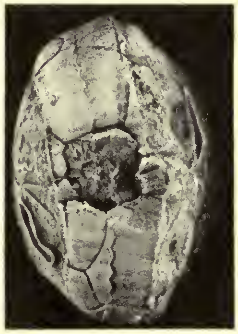

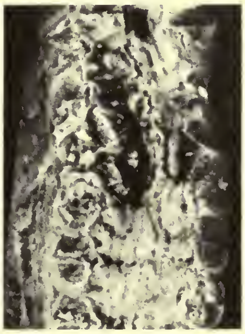

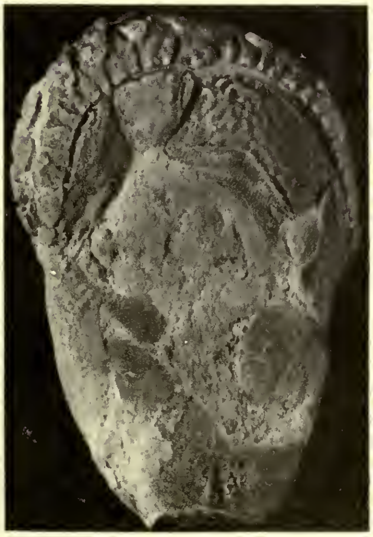
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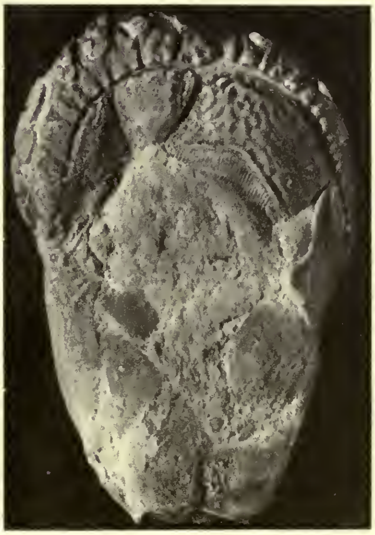

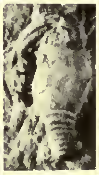
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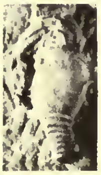

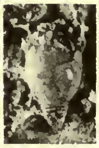
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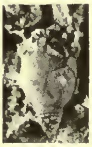


PLATE 4

Stereophotos of ***Pseudocrinites pyriformis*** sp. n.

Fig. 1. Lateral view of gonal face showing ornamentation of thecal plates and ambulacral flooring plates. Paratype, BU. H011.

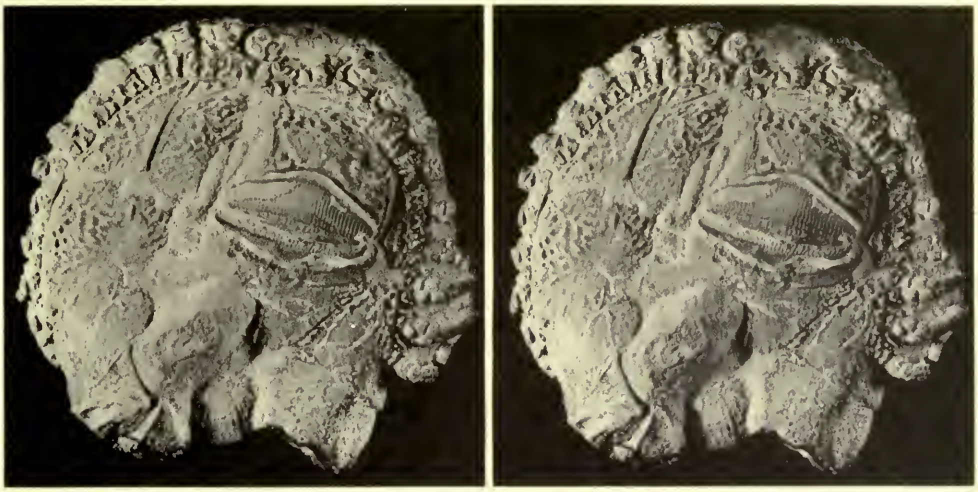
Fig. 2. Lateral view of ambulacrum 5 showing food grooves and ornamented cover plates. Holotype, BU. H010.

Fig. 3. Lateral view of ambulacrum 5 showing details of brachioles. Note the ornamented brachiolars. Paratype, BU. H011.

Fig. 4. Holotype, apical view. Note the arrangement of brachiole facets around the oral region.

Fig. 5. Same, abapical view showing cicatrix.

All ×2. All specimens whitened with ammonium chloride sublimate.



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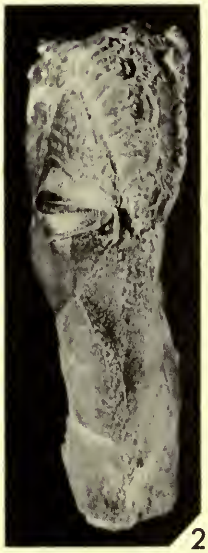

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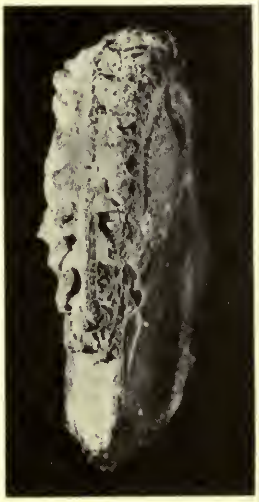

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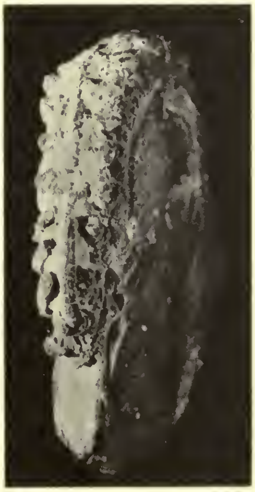

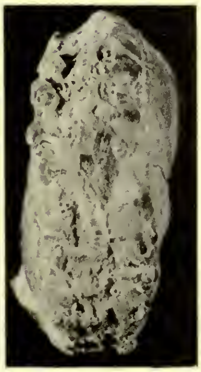

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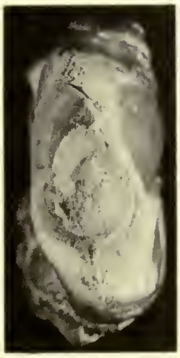

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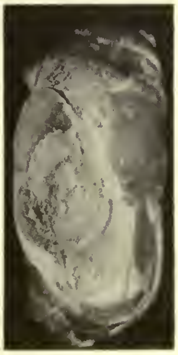


PLATE 5

Stereophotos of ***Tetracystis oblongus*** (Forbes), ***Apiocystites pentrematoides*** Forbes and ***Pseudocrinites pyriformis*** sp. n.

Pseudocrinites pyriformis sp. n.

FIG. 1. Lateral view of ambulacrum 2 which clearly terminates a long way from the cicatrix. BU. H010.

Tetracystis oblongus (Forbes)

FIG. 2. Lateral view of large specimen, showing some brachioles in ambulacrum to the right and in the ambulacrum to the left, the small brachiole facets and cover plates. SM. A.12603.

FIG. 3. Apical view of specimen BMNH. E.29075.

FIG. 4. Lateral view of ambulacrum 5, showing cover plates of main and lateral food grooves. BMNH. 57411.

FIG. 5. Right lateral view of Lectotype. SM. A.10140.

FIG. 6. Same, apical view, showing arrangement of food grooves around the mouth.

FIG. 7. Same, abapical view, showing ambulacra reaching the column.

FIG. 11. Same, anterior lateral view, showing ornamentation of thecal plates.

FIG. 12. Same, left lateral view.

FIG. 13. Same, posterior laterior view, showing periproct with asymmetrical circlet of auxiliaries.

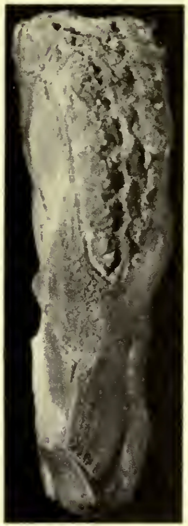
Apiocystites pentrematoides Forbes

FIG. 8. Abapical view showing ambulacra reaching the cicatrix. SM. A.12601.

FIG. 9. Abapical view of a weathered specimen showing growth lines of individual plates. (BU. unregistered).

FIG. 10. Apical view of same specimen showing growth lines of orals and ambulacral flooring plates. Cf. Text-fig. 32 ; Pl. 6, fig. 6.

All ×2. All specimens whitened with ammonium chloride sublimate.



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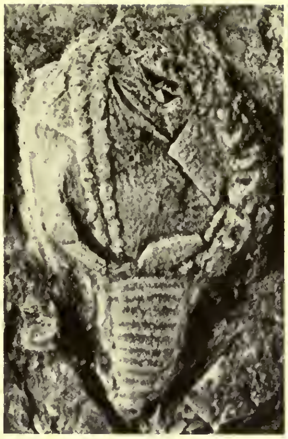

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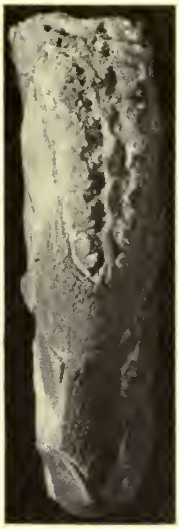

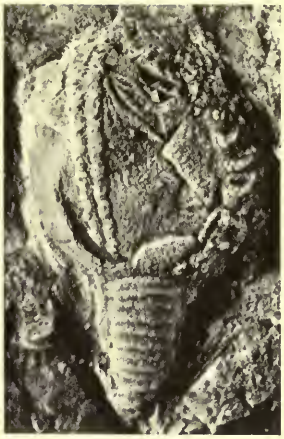

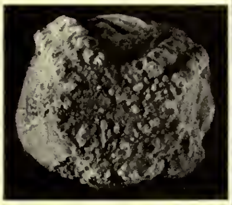

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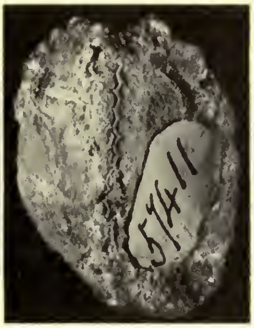

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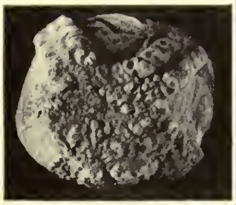

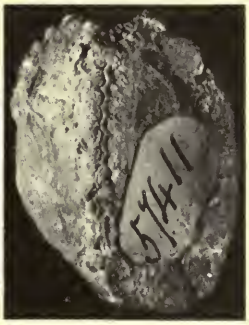

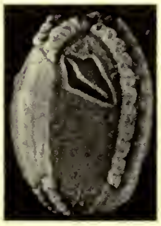

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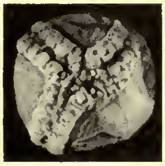

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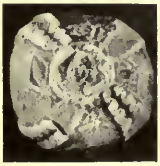

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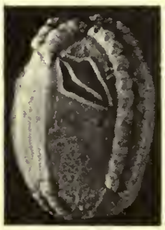

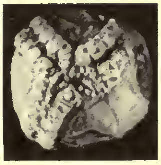

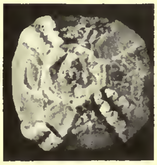

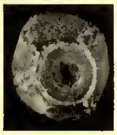

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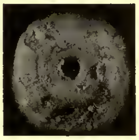

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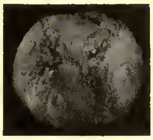

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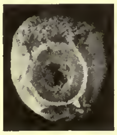

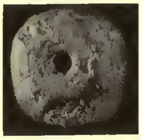

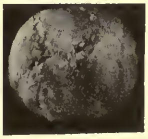

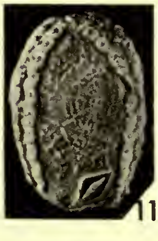

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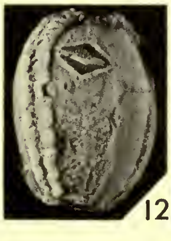

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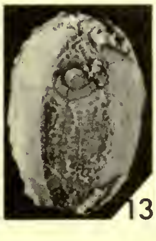

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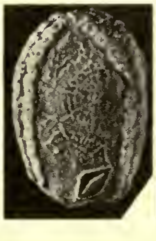
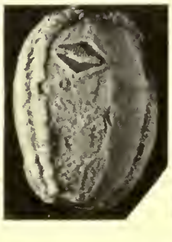




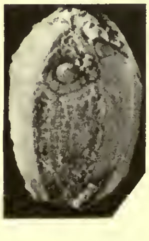


PLATE 6

Stereophotos of ***Apiocystites pentrematoides*** Forbes

FIG. 1. Anterior lateral view showing ambulacra level with thecal plates and tubercular flanges to outer proximals.

FIG. 2. Posterior lateral view showing anal pyramid and circlet of auxiliaries.

Fig. 3. Anterior lateral view.

FIG. 4. Posterior lateral view showing some colour bands.

FIG. 5. Right lateral view.

FIG. 6. Details of apical region. Note the oval mouth and seven oral plates. Cf. Text-fig. 32.

FIG. 7. Apical view. The anus is towards the observer and the gonopore and hydropore are to the left.

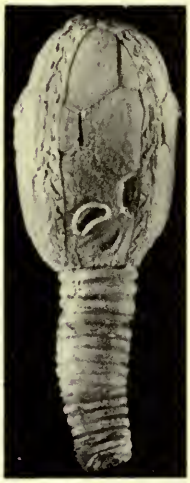
FIG. 8. Left lateral view.

FIG. 9. Right lateral view.

FIG. 10. Left lateral view showing ornamentation of thecal plates.

Fig. 6 ×4. All others ×2. All specimens whitened with ammonium chloride sublimate.

Figs. 1, 2, 5, 7, 10 (BMNH. E.29074) ; Figs. 3, 4, 6, 8, 9 (BU. unregistered, weathered specimen showing growth lines of thecal plates).



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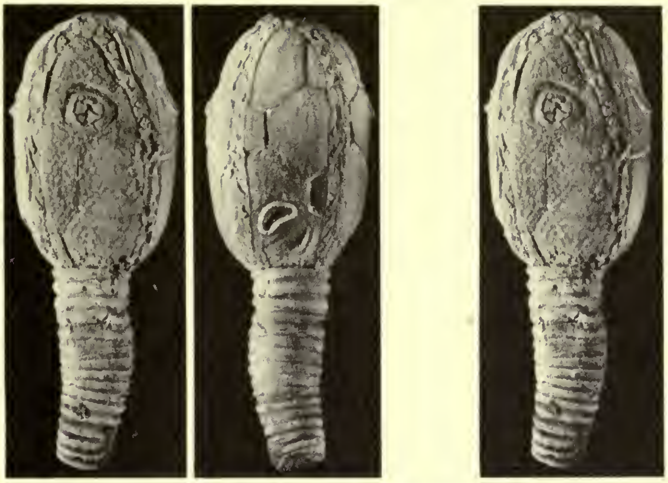

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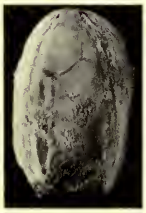

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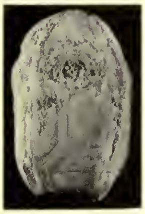

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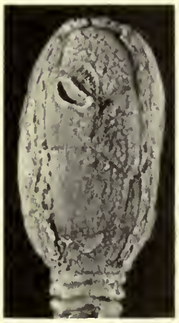

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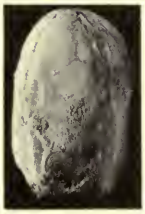

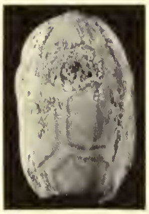

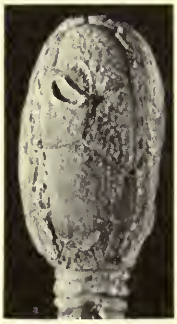

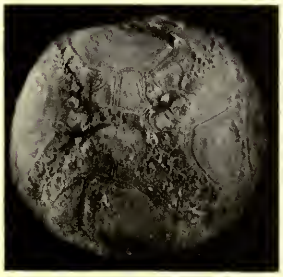

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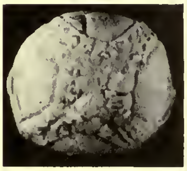

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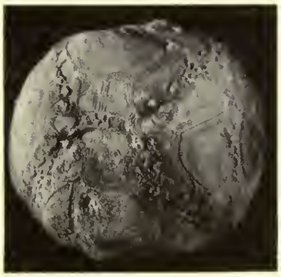

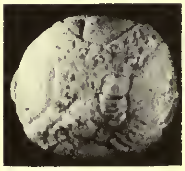

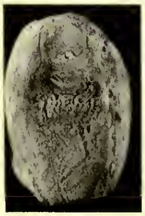

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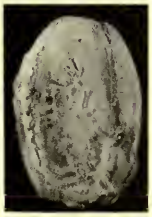

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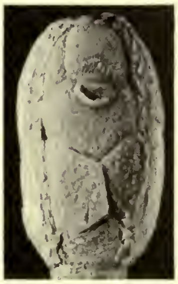

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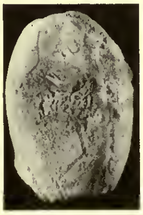

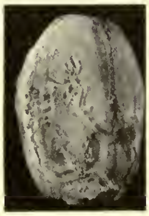

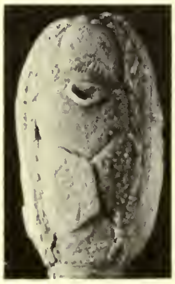

PLATE 7

Stereophotos of ***Apiocystites pentrematoides*** Forbes and ***Glansicystis baccata*** (Forbes)

Apiocystites pentrematoides Forbes

FIG. 1. Fairly complete specimen showing short stem terminating in a branched root structure. The distal portion of the stem is very short. BMNH. 48192.

Glansicystis baccata (Forbes)

FIG. 2. Apical view showing area occupied by orals and impression of one short ambulacrum on the radial plates.

FIG. 3. Abapical view showing cicatrix.

FIG. 4. Apical view showing the orals have the same ornamentation as the other thecal plates. Note there are three facets to the left and three or four to the right.

FIG. 5. Apical view showing the mouth. There are two facets to the right and three to the left.

FIG. 6. Posterior lateral view showing ornamentation of thecal plates.

FIG. 7. Left lateral view.

FIG. 8. Apical view. Note the very small area occupied by the orals, and the strong tubercular ornamentation.

FIG. 9. Left lateral view.

FIG. 10. Right lateral view.

FIG. 11. Posterior lateral view. Note there are four plates around the periproct (IL4, IL5, L4, L5) and there is another plate adoral to L5 which latter does not interrupt the radial circlet. Cf. Fig. 6 and Text-fig. 38.

FIG. 12. Abapical view showing the cicatrix.

FIG. 13. Right lateral view.

FIG. 14. Anterior lateral view. This specimen has the normal plating arrangement for the first four circlets.

FIG. 15. Anterior lateral view showing rhomb B2 : IL2 very well preserved.

FIG. 16. Right lateral view.

FIG. 17. Left lateral view.

FIG. 18. Posterior lateral view. Note that IL5 is set above and between ILL4 and 1 which are in contact, and that IL4 is above and between B4 and B1 causing B4 to be pentangular in outline. Cf. Figs. 6, 11 and Text-fig. 37.

Figs. 2–7, 13, 14, 16–18 common form ; Figs. 8–12, 15 typical form.

All × 2. All specimens whitened with ammonium chloride sublimate.

Figs. 2, 3, 6, 7, 13, 14 (BMNH. E.29058) ; Fig. 4 (BU. H055) ; Fig. 5 (OUM. C.518) ; Figs. 8–12, 15 (BMNH. E.29057) ; Figs. 16–18 (SM. A.12577).

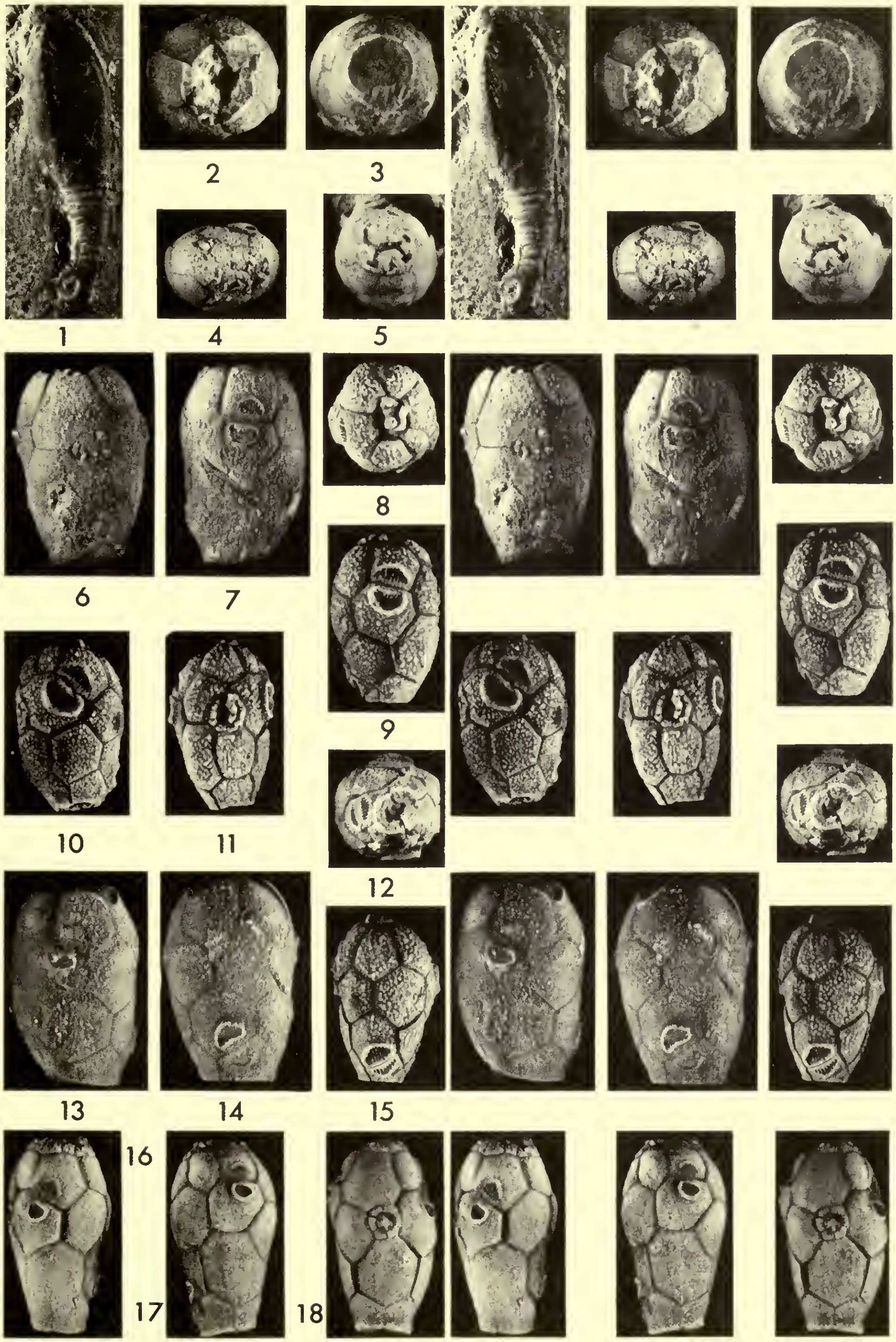
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PLATE 8

Stereophotos of ***Glansicystis baccata*** (Forbes), ***Prunocystites fletcheri*** Forbes and ***Schizocystis armata*** (Forbes)

Glansicystis baccata (Forbes)

Fig. 1. Anterior lateral view. SM. A.12577.

Fig. 2. Posterior lateral view showing a few brachioles preserved attached to the theca. BU. H063.

Fig. 3. Well preserved example showing a complete stem attached to polyzoan. Note flanges ornamented with tubercles on outer proximals. BU. H025.

Prunocystites fletcheri Forbes

Fig. 4. Holotype, showing some slender brachioles attached to the theca, and the ornamentation of thecal plates described by Forbes. This ornamentation is due to erosion. SM. A.10187.

Schizocystis armata (Forbes)

Fig. 5. Left lateral view showing one type of ornamentation of thecal plates. Note the hydropore and gonopore are not visible in this view. Cf. Pl. 9, fig. 7. SM. A.12592.

Fig. 6. Same, right lateral view showing well developed rhomb L4 : R3.

Fig. 7. Same, anterior lateral view showing well developed rhomb B2 : IL2. Note the adoral concavity of left side (to right of photo) and sinuous food groove in anterior ambulacrum.

Fig. 8. Right lateral view showing well developed rhomb L4 : R3 and four plates meeting at a point. Note ambulacra are confined to apical ridge and the periproct is very prominent. SM. A.10197.

Fig. 9. An internal mould showing faintly, the reticular structure described in the text. Cf. Text-fig. 44. SM. A.8137*a*. The specimen is inverted.

Fig. 10. Left lateral view showing thecal ornamentation, unusual shape to L1 and the pyramid of gonals over the gonopore. Note the slit-like hydropore and gonopore are not facing the observer, and that the anal pyramid is directed aborally and slightly towards the left of theca. SM. A.10197.

Fig. 11. Posterior lateral view showing the periproct and two or three facets to the left of posterior ambulacrum (right of photo.). SM. A.12592.

Figs. 2, 3 × 1. All others × 2. All specimens whitened with ammonium chloride sublimate.

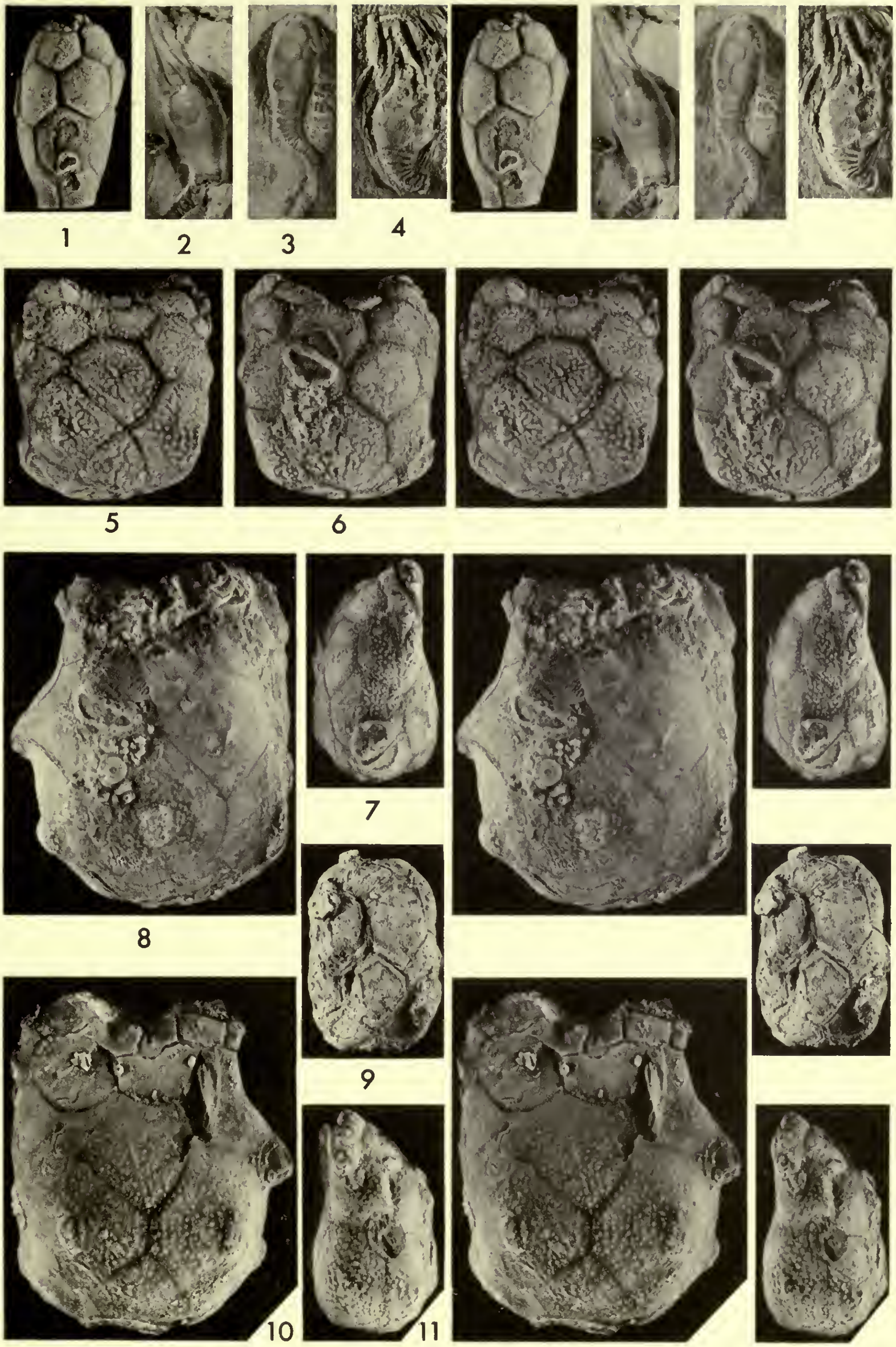
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PLATE 9

Stereophotos of ***Schizocystis armata*** (Forbes) and ***Prunocystites fletcheri*** Forbes

Schizocystis armata (Forbes)

FIG. 1. Apical view showing the hydropore and gonopore clearly. Note the brachiole facets are primarily towards the observer in ambulacrum to the left and away from the observer in the other ambulacrum. SM. A.12592.

FIG. 2. Same, abapical view showing cicatrix and rhomb B2 : IL2. Note if the theca lay on the side towards the observer then B2 : IL2 would be raised off the surface.

FIG. 3. A crushed theca showing ornamentation of large prominent tubercles and radiating ridges. Cf. Fig. 5 and Pl. 8, figs. 5, 10. BMNH. 57402.

FIG. 4. An oblique view of posterior ambulacrum showing curved food groove. Note there are no facets to the left of photo. BMNH. E.7571.

FIG. 5. Three-rhombed form showing ornamentation of fine regular tubercles on right lateral face. BMNH. 57410.

FIG. 6. Oblique view of anterior ambulacrum showing longer food groove and only one facet on left of photo. Note in this two-rhombed specimen the gonopore and hydropore are facing apically and not to the left. BMNH. E.7571.

FIG. 7. Left lateral view showing thecal ornamentation and rhomb L1 : R5. In this three-rhombed specimen the gonopore and hydropore face to the left. BMNH. 57410.

FIG. 8. Internal mould showing cast of oesophagus apically and of gonopore and hydropore just below it. SM. A.8138*a*.

FIG. 9. Well preserved example showing almost complete stem. Note tubercular flanges on outer proximals and larger distals. BMNH. 57442.

Prunocystites fletcheri Forbes

FIG. 10. Large specimen, possibly belonging to *P. fletcheri*, showing well developed ambulacrum of the type found in the Staurocystinae. Note the rhomb is angular and imperfectly disjunct, and also the slender brachioles. BU. IVa 25.

FIG. 11. Another relatively large theca with part of the stem preserved. Note the flanges on the outer proximals are smooth. BMNH. 57395.

Fig. 9 × 1. All others × 2. All specimens, except Fig. 8, whitened with ammonium chloride sublimate.

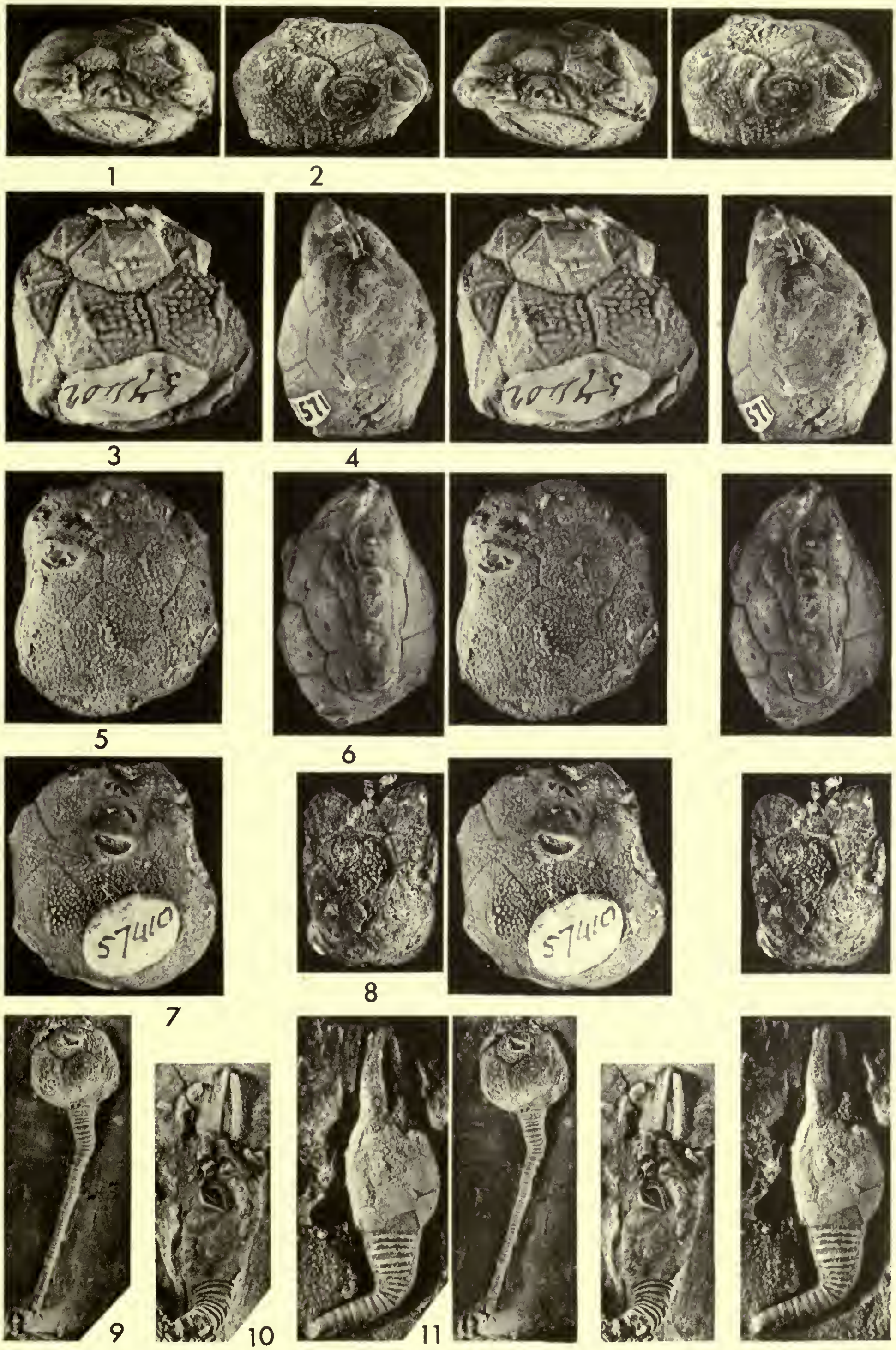
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PLATE 10

Staurocystis quadrifasciatus (Pearce)

Fig. 1. Specimen showing complete stem and root structure. × 1. Whitened with ammonium chloride sublimate. BMNH. E.7553.

Fig. 2. Section showing ambulacrum (right) and rhomb B2 : IL2. BMNH. E.16353, × 5.

Fig. 3. Specimen showing detail of dichopores in the pectinirhomb. BMNH. E.16353, × 15.

Fig. 4. Specimen with long incomplete stem. BU. H022, × 1. Whitened with ammonium chloride sublimate. Cf. Fig. 5.

Fig. 5. Another specimen with very short stem. BU. H019, × 1. Whitened with ammonium chloride sublimate.

Fig. 12. Specimen showing poorly developed colour banding in thecal plates. BU. H042, × 2. Photographed under water.

Tetracystis oblongus (Forbes)

Fig. 6. Left lateral view of theca showing well developed colour banding in L1, IL1 and R5. SM. A.11160, × 2. Photographed under water.

Fig. 13. Right lateral view showing part of stem (possibly belonging to this theca). Note the colour banding in B3, IL3 and stem. SM. A.11160, × 2. Photographed under water.

Pseudocrinites bifasciatus Pearce

Fig. 7. View of interior of thecal plates of gonal face showing colour banding. BMNH. 47833, × 2. Photographed under water.

Fig. 8. Specimen showing brachioles and complete stem ending in a root structure. BMNH. 40189, × 1. Whitened with ammonium chloride sublimate.

Apiocystites pentrematoides Forbes

Fig. 9. Fairly complete specimen showing short stem and weak colour banding in thecal plates. BMNH. 40188, × 2. Whitened with ammonium chloride sublimate.

Fig. 14. Another specimen showing complete stem terminating in root structure. SM. A.12599, × 1. Whitened with ammonium chloride sublimate.

Glansicystis baccata (Forbes)

Fig. 10. Apical view showing small area occupied by oral plates and the food grooves. Lectotype, GSM. 7380, × 2. Whitened with ammonium chloride sublimate.

Fig. 11. Same, posterior lateral view showing characteristic ornamentation of thecal plates in the typical form of this species. × 2. Whitened with ammonium chloride sublimate.

Schizocystis armata (Forbes)

Fig. 15. Right lateral view showing prominent umbones of the ILL plates and periproct directed aborally. Lectotype, GSM. 7381, × 2. Whitened with ammonium chloride sublimate.

Fig. 16. Two specimens preserved together showing a fairly complete stem (C.397) and brachioles (C.398). OUM. C.397–98, × 1 approx. Whitened with ammonium chloride sublimate.

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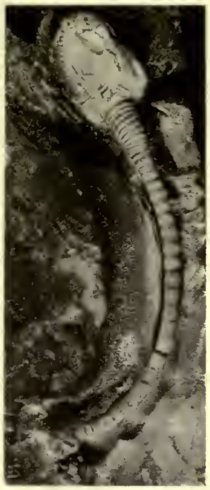
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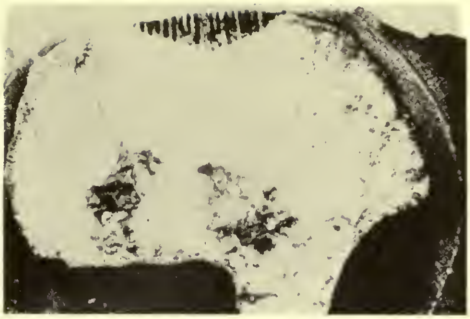
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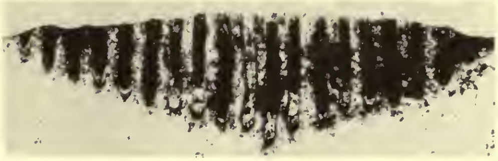
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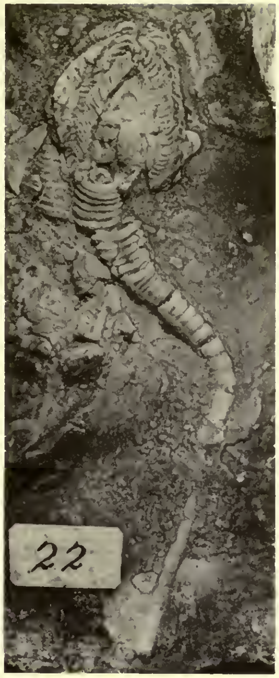

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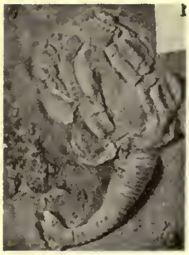
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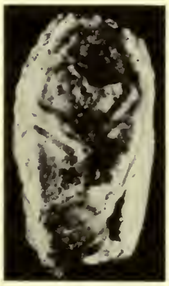
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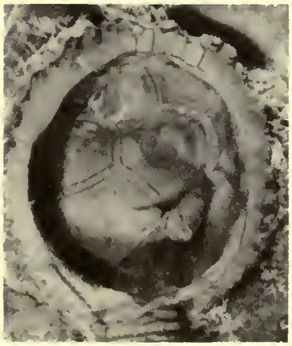
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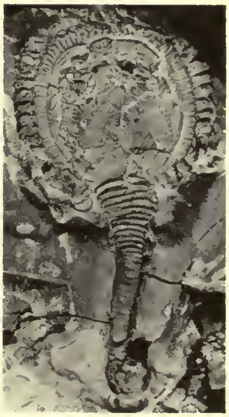
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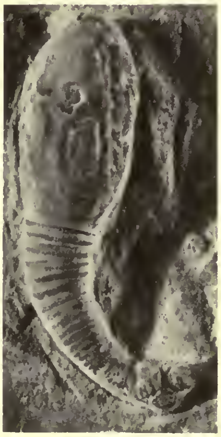
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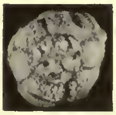
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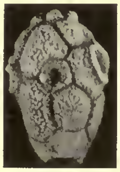
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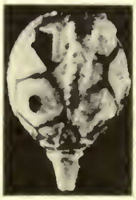
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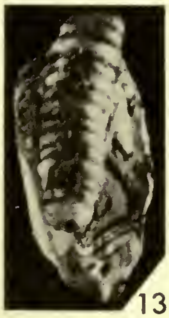
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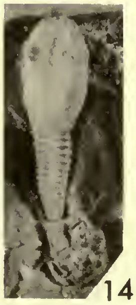
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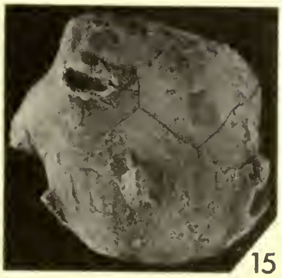
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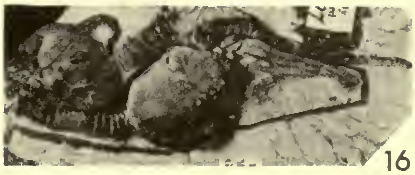
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